

Reappraisal of the Postcranium of *Hadropithecus* (Primates, Indroidea)

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ABSTRACT *Hadropithecus stenognathus* (Lorenz von Liburnau [1899] Anz. Akad. Wiss. Wien 36:255–257), a giant extinct lemur from Madagascar, has been reconstructed as primarily terrestrial and probably cursorial on the basis of its postcranial anatomy, especially long bone gracility and interlimb proportions. We show here that aspects of this reconstruction are almost certainly incorrect. Hindlimb bones of *Archaeolemur* have been misattributed to *Hadropithecus*, and new hindlimb allocations (including newly recognized elements such as the calcaneus) indicate that *Hadropithecus* had a robust body build and lacked osteological specializations for cursoriality. We review the evidence for the existence of “*Bradylemur*” and offer a view of archaeolemurid positional behavior that includes terrestrial and arboreal components. Body size and limb proportions of *Hadropithecus* are reassessed in light of our new allocations. Am J Phys Anthropol 103:529–556, 1997. © 1997 Wiley-Liss, Inc.

The Archaeolemuridae is one of the best known of extinct Malagasy lemur families; it belongs to the superfamily Indroidea, along with the extinct Palaeopropithecidae (the sloth lemurs *Archaeoindris*, *Palaeopropithecus*, *Babakotia*, and *Mesopropithecus*) and the extant Indridae (*Propithecus*, *Indri*, and *Avahi*). Hundreds of archaeolemurid specimens have been recovered from subfossil sites located through all parts of Madagascar with the exception of the eastern rainforest. Three species are currently recognized: *Archaeolemur edwardsi* (from central Madagascar), *A. majori* (from southern and southwestern Madagascar), and *Hadropithecus stenognathus* (a rare though geographically widespread species, from southern, western, and central Madagascar). New specimens from the north of Madagascar (e.g., the caves of the Ankarana Massif and the Mahajanga Plateau) have skulls that are marginally larger than *Archaeolemur edwardsi* and

an apparently unique set of postcranial proportions. They are currently under study.

A review of archaeolemurid specimens in museum collections reveals examples from southern, southwestern, and central Madagascar that cannot be accommodated into any species *as currently described*. A re-examination of prior attributions of these and other specimens is in order, especially as they relate to *Hadropithecus*.

The problematic specimens are housed in the collections of the Paleontology Department of the British Museum [Natural His-

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tory] London (BMNH); the Paleontology Department of the Vienna Naturhistorisches Museum (VNM); the Institut de Paléontologie and Laboratoire d'Anatomie Comparée at the Muséum National d'Histoire Naturelle, Paris (MNHN); and the Université d'Antananarivo Laboratoire de Paléontologie des Vertébrés, Madagascar (UALPV).¹ They include a calcaneus in good condition, a fragmentary pelvis, several partial femoral shafts, and a nearly complete femur.

The calcaneus (BMNH M7946) was found at Andrahomana (a coastal cave in south-east Madagascar) at the turn of the 20th century. Specimens collected at Andrahomana were distributed to museums in London, Vienna, and Madagascar. The site yielded bones of living lemurs (including *Lemur catta*) alongside those of giant extinct lemurs (*Megaladapis*, *Archaeolemur*, *Pachylemur*, and *Hadropithecus*) and other mammals (*Cryptoprocta*, *Hippopotamus*).

Walker (1967) was the first paleontologist to describe the calcaneus. Impressed by its large size, he allocated it to *Megaladapis madagascariensis*. At that time, the calcaneus of *Megaladapis* was unknown. In the late 1980s and early 1990s, paleontological expeditions to cave sites in northern Madagascar yielded associated foot bones of *Megaladapis* sp. (cf. *grandidieri*/*madagascariensis*), including complete calcanei (Simons et al., 1990; Wunderlich et al., 1996). Recent excavations at the southwestern site of Ankililolo yielded most of the hindlimb of a subadult *M. madagascariensis*, including a calcaneus. The discovery of associated foot bones of *Megaladapis* indicated that Walker's earlier allocation of the Andrahomana calcaneus to *Megaladapis madagascariensis* was incorrect.² The distinctive morphology of the Andrahomana calcaneus is not that of a megaladapid; it is that of a robust archaeolemurid (Wunderlich et al., 1996).

In 1977, Godfrey noted the presence in the Andrahomana collections of the Vienna Naturhistorisches Museum of a large though

fragmentary archaeolemurid pelvis (VNM 1934.IV.48a and b). She suggested that this specimen, too large to be *Archaeolemur majori*, might belong instead to *Hadropithecus stenognathus*, which was also found at Andrahomana. However, she recognized that this interpretation would force a rejection of Lamberton's (1938) hindlimb attributions for *Hadropithecus*.

Grandidier (1902a, 1905) figured and described a robust femur from Belo (in western Madagascar) that is housed at the Paris museum (1905, Plate 9). The specimen is considerably larger overall and is flatter at its midshaft than that of *Archaeolemur majori* from the same site (Grandidier, 1905, Plate 12). Grandidier assigned the larger specimen to *Palaeopropithecus ingens*.³ It wasn't until true postcrania of *Palaeopropithecus* were recognized as such (Carleton, 1936, 1937; Lamberton, 1947; see Simons et al., 1992, for a review) that this specimen was identified as an archaeolemurid. Carleton (1936) allocated it to *Bradylemur robustus*, a nomen that had been erected for other specimens from the same site (Grandidier, 1899, 1902b), but that had long since been synonymized with *Archaeolemur* (Standing, 1908).

In the early 1980s, subfossil postcrania in the collections of the Académie Malgache were transferred to the Université d'Antananarivo and catalogued under the direction of M. Vuillaume-Randriamanantena. Among these were a number of specimens that Vuillaume-Randriamanantena (1982; pers. commun.) took to belong to Carleton's robust archaeolemurid, *Bradylemur robustus*. They included a half dozen huge but damaged archaeolemurid femora (A1–A6) from Anavoha in southwestern Madagascar and two even larger specimens (A7, A8) apparently from Ampasambazimba in central Madagascar.

The calcaneus, pelvis, and femora suggest the existence of an archaeolemurid species (distributed through southern, western, and central Madagascar) that was much larger in body size than any of the currently accepted species. There is an alternative possibility, however—that these are hindlimb bones of *Hadropithecus stenognathus*. If this

¹The extensive subfossil lemur collections of the Académie Malgache were recently transferred to the Université d'Antananarivo Laboratoire de Paléontologie des Vertébrés.

²This calcaneus is the only presumed record of *Megaladapis madagascariensis* at Andrahomana. All other megaladapid specimens from Andrahomana belong to *M. (Peloriadapis) edwardsi* (see Vuillaume-Randriamanantena et al., 1992).

³This mistaken allocation was unfortunately repeated by Sera (1935, Fig. 2) and Szalay and Delson (1979).

is the case, then it follows that the considerably more gracile hindlimb bones that Lamberton (1938) attributed to *Hadropithecus* have been misallocated. It also follows that prior accounts of the limb proportions and postcranial adaptations of *Hadropithecus* (along with body masses based on Lamberton's allocations) are incorrect (e.g., Jolly, 1970; Walker, 1974; Vuillaume-Randriamanantena, 1982; Godfrey, 1988; Godfrey et al., 1995).

We argue below that these specimens do indeed belong to *Hadropithecus*. We believe that Lamberton incorrectly allocated to *Hadropithecus* femora, tibiae, and fibulae that actually belong to *Archaeolemur majori*. While unequivocal confirmation of our argument must await the discovery of associated skeletal materials of *Hadropithecus*, we believe that the evidence in favor of our interpretation is compelling.

Our task in this paper is threefold: 1) to review current hindlimb attributions for *Hadropithecus* and show why they are problematic; 2) to describe the calcaneus, pelvis, and femora that we believe actually belong to *Hadropithecus* but have been previously attributed to *Bradylemur robustus* or other lemur taxa; and 3) to review and evaluate other postcranial as well as craniodental specimens that have been attributed to *Bradylemur robustus* but clearly do not belong to *Hadropithecus*.

CURRENT HINDLIMB ALLOCATIONS: LAMBERTON'S *HADROPITHECUS*

Historical attributions and the issue of intrageneric variation

Lorenz von Liburnau (1899) assigned the nomen *Hadropithecus stenognathus* to a right mandible from Andrahomana (southeast Madagascar); the specimen is housed at the Vienna Naturhistorisches Museum. Shortly thereafter, he ascribed to *Hadropithecus* several long bones including two humeri (VNM 1934.IV.30 and 1934.IV.29a), a radius (VNM 1934.IV.29b), and an ulna (VNM 1934.IV.29c), as well as a few partial ribs and other fragments of the axial skeleton (Lorenz von Liburnau, 1901).⁴ There were no hindlimb bones in the lot.

Similarities between *Hadropithecus* and *Archaeolemur* were soon documented (Major, 1900; Lorenz von Liburnau, 1901, 1902; Grandidier, 1902b, 1905; see Tattersall, 1973, for a review). Standing (1908) assigned both genera to a subfamily of the family Indridae (the Archaeolemurinae); Szalay and Delson (1979) gave this group independent familial status.

In 1938, Charles Lamberton wrote a monograph on *Hadropithecus*. By this time, additional forelimb and craniodental specimens of *Hadropithecus* had been recovered from sites in central Madagascar (Ampasambazimba), western Madagascar (Tsirave, Ampoza-Ankazoabo, Belo), and the southwest (Anavoha), but still no hindlimb bones had been described. Lamberton tried to remedy the situation. He assigned to *Hadropithecus* one femur, two tibiae, and two fibulae from Tsirave in western Madagascar and one tibia and fibula from Anavoha in the extreme southwest (Lamberton, 1938). While he expressed reservations concerning his hindlimb allocations (1938),⁵ he nevertheless defended them based on subtle distinctions in size and morphology. No records of associations with forelimb bones or crania of either *Archaeolemur* or *Hadropithecus* exist for any of these specimens.

Lamberton's comparisons of his "*Hadropithecus*" postcrania with *Archaeolemur majori* and *A. edwardsi* were based on small samples. More comprehensive tests utilizing larger samples of *Archaeolemur* demonstrate the inadequacy of Lamberton's comparisons. For example, on the basis of a sample of 10, Lamberton reported the femur of *Archaeolemur majori* as ranging from 157.2 to 165.8 mm in length. Contrasting this with a single value (172 mm) for "*Hadropithecus*" from Tsirave and a single value (185.5 mm) for *A. edwardsi* from Ampasambazimba, he concluded that the hindlimb of *Hadropithecus* was longer than that of *Archaeolemur majori* but shorter than *A. edwardsi*. Our more comprehensive sample of 38 *Archaeolemur* femora from southern and western Madagascar ranges from 143.4 to 178 mm; 18 femora of *Archaeolemur* from central Madagascar (Ampasambazimba, An-

⁴Some of his allocations were incorrect; for example, originally allocated to *Hadropithecus* was a portion of a shaft of a right humerus of an *Archaeolemur* (VNM 1934.IV.29/11).

⁵Lamberton (1938:161) wrote, "Nous rapporterons ces divers ossements à l'*Hadropithecus*, sans avoir cependant la pleine certitude que notre attribution est exacte."

TABLE 1. Comparison of femoral dimensions (in mm) of *Archaeolemur* and Lamberton's "Hadropithecus" (Southern and Western Madagascar only)

	n	Min	Max	Mean	Standard error
Midshaft transverse diameter					
<i>Archaeolemur</i>	59	13.9	19.4	15.9	0.149
Lamberton's "Hadropithecus"	5	14.1	15.5	14.8	0.249
<i>t</i> -test: df = 62, <i>t</i> = 2.15, <i>P</i> < .05					
Midshaft anteroposterior diameter					
<i>Archaeolemur</i>	59	11.3	15.6	13.3	0.119
Lamberton's "Hadropithecus"	5	11.7	14.5	13.3	0.510
<i>t</i> -test: df = 62, <i>t</i> = -0.009, NS					
Maximum length					
<i>Archaeolemur</i>	34	143.4	175.0	160.8	1.359
Lamberton's "Hadropithecus"	5	158.2	178.0	168.4	3.500
<i>t</i> -test: df = 37, <i>t</i> = -1.998, NS					
Femoral head superoinferior diameter					
<i>Archaeolemur</i>	40	17.3	22.4	20.3	0.177
Lamberton's "Hadropithecus"	3	18.5	20.2	19.5	0.524
<i>t</i> -test: df = 41, <i>t</i> = 1.175, NS					

tsirabe, Masinandrana) fall between 165 and 194.5 mm. There is a strong geographic component to size variation manifested in virtually every major skeletal element of *Archaeolemur* (Table 1; see also Godfrey and Petto, 1981; Godfrey et al., 1990; Albrecht et al., 1990; Albrecht and Miller, 1993). Specimens from the south tend to be smaller than those from the west, which are in turn smaller on average than specimens from central or northern Madagascar. Lamberton's "Hadropithecus" femur from Tsirave (172 mm) falls well within the range of variation of *Archaeolemur* from the same site (161–178 mm); it is also shorter than the longest femur of *Archaeolemur* from the extreme south (174.6 mm), and longer than the shortest femur from Ampasambazimba (165 mm). Similarly, Lamberton's "Hadropithecus" tibiae and fibulae are "long" only in comparison to most *A. majori* from the south. They fall squarely within the range of variation of *Archaeolemur* from the west. Clearly, Lamberton did not consider within-site variability or geographic variation in making his taxonomic assessments.

Lamberton's defense of the morphological distinctiveness of his "Hadropithecus" hindlimb specimens is equally weak. Lamberton (1938) maintained that the femur of *Hadropithecus* differs from that of *Archaeolemur* in having a slightly more slender shaft, smaller head, and longer neck. He described the shaft as more anteroposteriorly bowed (in lateral view) and squarer in cross-section (i.e., less anteroposteriorly flattened) than is typical for *Archaeolemur*; the femoral condyles as more disparate in size; the patellar trochlea as wider and deeper; and the intercondylar groove as wider. Each of these presumably distinguishing traits is variable in *Archaeolemur*; specimens identified as *Hadropithecus* simply fall at one end of *Archaeolemur*'s range of variation.

Geographically controlled statistical comparisons reveal just how similar Lamberton's "Hadropithecus" hindlimb bones are to those of *Archaeolemur* (Table 2).⁶ Many parameters (e.g., femoral midshaft anteroposterior diameter, maximum femur length, femoral head diameter) show no statistical difference. Others show marginally significant difference. For example, Lamberton's "Hadropithecus" femora are slightly narrower and squarer at the midshaft than are *Archaeolemur* femora from the same sites. (Given that a slender shaft was a primary criterion for diagnosing "Hadropithecus," this result is hardly surprising.) In contrast, the forelimb and crania of *Hadropithecus* differ markedly from those of *Archaeolemur*; as is easily demonstrated statistically or graphically (cf. Figs. 1 and 2). Whereas it is not unusual for closely related species to resemble one another in their postcranial anatomy, the craniodental and forelimb distinctions of *Archaeolemur majori* and *Hadropithecus stenognathus* are so striking that it is difficult to imagine their hindlimbs being so similar, not only in morphology, but also in absolute size.

⁶Our "Hadropithecus" sample includes specimens that Vuillaume-Randriamanantena assigned to *Hadropithecus* during the early 1980s when she inventoried the 2,000 postcranial specimens of giant lemurs in the collection of the Académie Malgache. These are FAL69 from Tsirave, FHP3 and FHP4 from Manombo Tulear, and FAL42 and FAL56 from Ampasambazimba.

TABLE 2. Descriptive statistics and ANOVAs for postcrania of *Archaeolemur*, by site

Site (n)	Region	Mean (mm)	Min	Max
Femur length (n = 68)				
Bevoha (3)	Southwest	150.3	146.0	159.0
Andrahomana (5)	Southeast	153.8	143.4	162.8
Anavoha (15)	Southwest	161.0	149.0	174.6
Ambolisatra (3)	Southwest	163.6	158.2	170.7
Bemafandry (1)	Southwest	165.0	—	—
Tsirave (11)	West	168.4	161.0	175.0
Lamboharana (1)	Southwest	168.6	—	—
Ankarana (9)	North	174.6	164.3	190.0
Masinandriana (2)	Central	177.0	177.0	177.0
Morarano (2)	Central	178.0	178.0	178.0
Ampasambazimba (14)	Central	182.3	165.0	194.5
Mahajanga (2)	Northwest	183.0	178.2	187.8
Humerus length (n = 56)				
Taolambiby (1)	Southwest	126.5	—	—
Andrahomana (8)	Southeast	131.4	123.1	147.0
Bevoha (3)	Southwest	131.5	127.0	135.0
Anavoha (14)	Southwest	136.8	126.0	149.0
Bemafandry (1)	Southwest	139.0	—	—
Ankarana (12)	North	139.7	132.0	155.0
Tsiandroina (1)	Southwest	141.5	—	—
Tsirave (5)	West	142.0	139.0	148.0
Morarano (1)	Central	145.5	—	—
Mahajanga (2)	Northwest	151.3	147.6	155.0
Ampasambazimba (8)	Central	152.7	143.0	164.0

One-way ANOVA for four sites with n > 8, femoral lengths by site

	N	Mean (mm)	SD
Anavoha (Southwest)	15	161.0	6.5
Tsirave (West)	11	168.4	5.1
Ankarana (North)	9	174.6	7.9
Ampasambazimba (Center)	14	182.3	9.1
All	49	171.2	11.1
F-value 21.516 (df 3, 45) $P < .001$			

One-way ANOVA for four sites with n > 7, humeral lengths by site

	N	Mean (mm)	SD
Andrahomana (Southeast)	8	131.4	7.7
Anavoha (Southwest)	14	136.8	6.4
Ankarana (North)	12	139.7	7.0
Ampasambazimba (Center)	8	152.7	6.7
All	42	139.6	9.7
F-value 14.312 (df 3, 38) $P < .001$			

Contradictory body mass and functional signals

The striking resemblance of Lamberton's "*Hadropithecus*" hindlimb bones to those of *Archaeolemur majori* suggests that Lamberton assigned bones of the latter species to *Hadropithecus stenognathus*. An even more compelling argument against Lamberton's allocations is that they are biomechanically implausible. Numerous postcranial features indicate that *Hadropithecus* converged on Old World monkeys and that terrestrial quadrupedalism was a dominant component of its locomotor repertoire. On the basis of a comparison of features of the forelimb (e.g.,

lower and more strongly posteriorly directed ulnar olecranon process, straighter radial shaft), Walker (1974) reconstructed *Hadropithecus* as more terrestrial than *Archaeolemur*. But Lamberton's hindlimb bones are considerably smaller than might be expected for a semiterrestrial quadruped with forelimbs and crania equal in size to those of *Hadropithecus stenognathus*.

This size disparity is evident when elements from different body parts are used to estimate the body mass of *Hadropithecus*. For example, using Lamberton's femoral allocations and regressions based on femoral head size, Godfrey et al. (1995) estimated

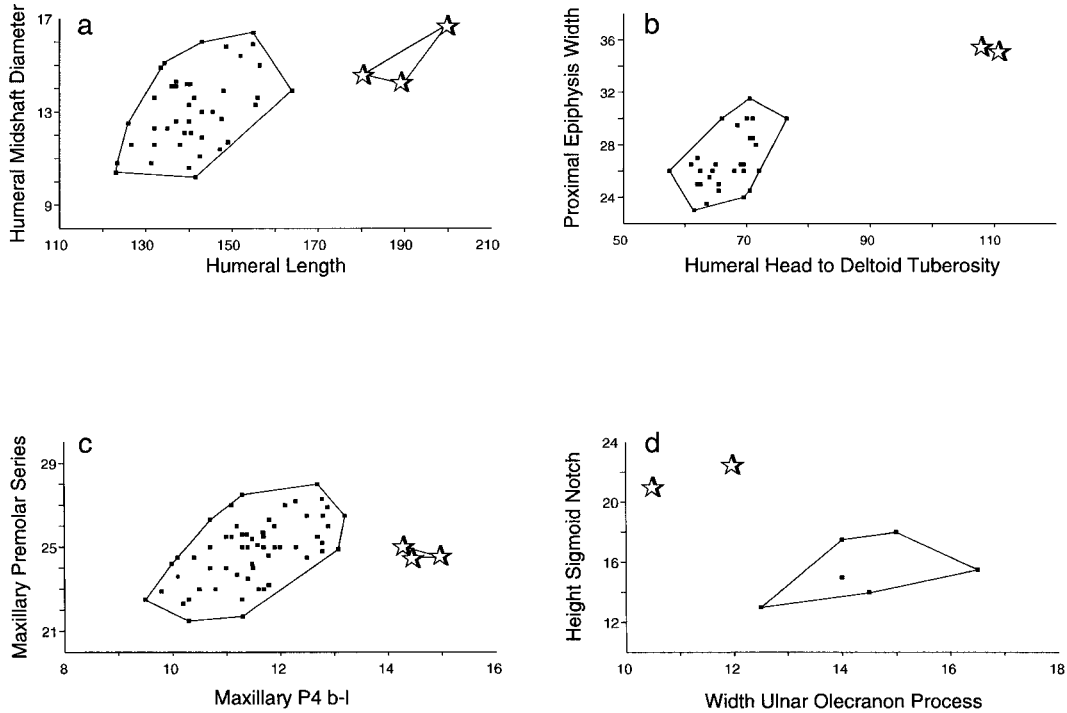


Fig. 1. Scatterplots of dental and forelimb dimensions reveal *Archaeolemur* (solid squares, mixed species) and *Hadropithecus* (open stars) as distinct clusters. **a:** Humeral midshaft transverse diameter (Y) vs. humeral length (X). **b:** Width of the proximal humeral epiphysis (Y) vs. distance from the humeral head to the

deltoid tuberosity (X). **c:** Length of the maxillary premolar series (Y) vs. buccolingual diameter of P⁴ (X). **d:** Height of the ulnar sigmoid notch (coronoid process to olecranon beak, Y) vs. width of the ulnar olecranon process (X). All measurements in mm.

the body mass of *Hadropithecus stenognathus* at 10.9 kg—slightly below the corresponding estimate for *A. majori* (11.6).⁷ Using Gingerich's molar-based regressions for estimating body mass, Fleagle (1988) calculated a body mass of 47 kg for *Hadropithecus stenognathus*! Whereas it is not unusual for different body parts to yield different mass signals (the archaeolemurids in general have relatively small femoral heads and *Hadropithecus* has exceptionally large molars), this much disparity is rare, and supports the inference of mistaken allocation.

Lamberton's allocations make *Hadropithecus* a peculiarly proportioned primate with contradictory functional signals. No terrestrial cercopithecoid exhibits this large a hu-

merus coupled with this small a femur. Accepting Lamberton's allocations, Demes and Jungers (1993b) found no parallel among cercopithecoid primates for the relationship in *Hadropithecus* between humeral and femoral midshaft cross-sectional geometries. Godfrey et al. (1995) found no monkey parallel for the humerofemoral length or head surface area indices of *Hadropithecus* (i.e., the ratios of humeral to femoral length and humeral to femoral caput surface areas, each expressed as a proportion). Their estimate for the humerofemoral length index of *Hadropithecus* (116) lies well above the maximum for cercopithecoids. The humerofemoral head surface area index of *Hadropithecus* (149) not only exceeds the range for terrestrial quadrupedal monkeys, but it exceeds the maximum for suspensory primates. Among mammalian quadrupeds in general, only some fossorial species exhibit compa-

⁷Using regressions based on humeral and femoral circumference, again with Lamberton's allocations for *Hadropithecus* femora, the estimates are 16.7 kg for *Hadropithecus* and 13.9 kg for *A. majori* (Godfrey et al., 1995). Fleagle's (1988) molar-based estimate for the body mass of *A. majori* is 17 kg.

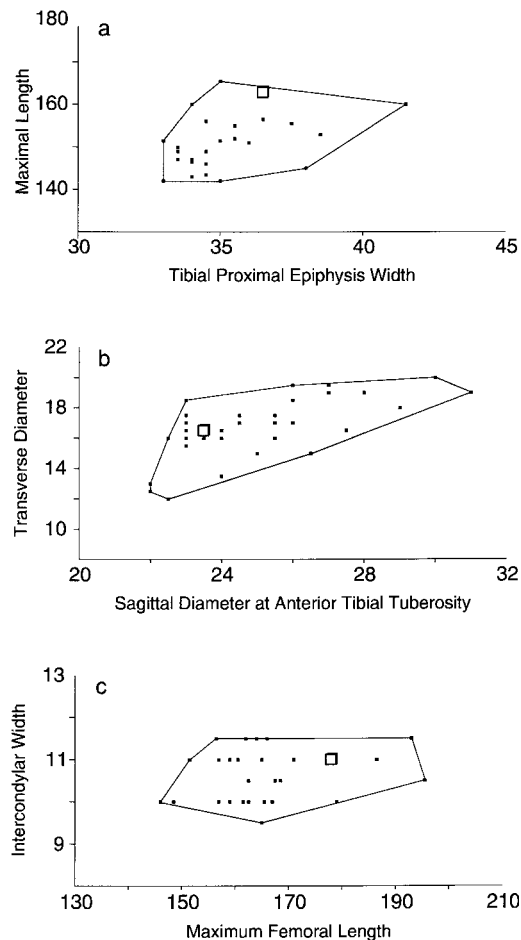


Fig. 2. Scatterplots of hindlimb dimensions fail to distinguish *Archaeolemur* (solid squares) from specimens attributed by Lambertson and others to "*Hadropithecus*" (open squares). **a:** Maximum tibial length (Y) vs. tibial proximal epiphysis width (X). **b:** Transverse diameter at the anterior tibial tuberosity (Y) vs. sagittal diameter at the anterior tibial tuberosity (X). **c:** Width of the femoral intercondylar fossa (Y) vs. maximum femoral length (X). All measurements in mm.

erable size disparity of the shoulder and hip joints. But nothing in the morphology of either the humerus or the alleged femur of *Hadropithecus* suggests fossoriality.

Most authorities on Malagasy subfossils accepted Lambertson's allocations because there did not appear to be an alternative (but see reservations expressed by Walker, 1974, and Godfrey, 1977). It furthermore seemed possible to rationalize Lambertson's aberrant reconstruction on the grounds that

highly terrestrial monkeys (such as gelada baboons) tend to have relatively long forelimbs (Jolly, 1970; Walker, 1974; Szalay and Delson, 1979; Tattersall, 1982). Some researchers took the presumed gracility of the limb bones of *Hadropithecus* as evidence of terrestrial cursoriality. Specifically, *Hadropithecus* was compared to the most cursorial of terrestrial primates, *Erythrocebus patas*, the patas monkey.

Unfortunately, the argument that *Hadropithecus* was a terrestrial cursor is contravened even by the evidence of the forelimb. For example, the deltoid tubercle of the humerus and bicipital tubercle of the radius are distally situated in all archaeolemurids, and more distally situated in *Hadropithecus* than in *Archaeolemur*. Clearly, there was no proximal concentration of the propulsive muscle mass (as is common among cursorial mammals; see Smith and Savage, 1955; Hildebrand and Hurley, 1985). *Hadropithecus* has an exceptionally low brachial index (84, cf. 104–105 for *Archaeolemur*); see Table 3. Brachial indices are highly variable in anthropoids, and the significance of that variability is unclear. However, relative elongation of the more distal limb elements is often considered a hallmark of cursoriality in mammals in general (Hildebrand, 1995), and baboons and patas monkeys tend to have relatively high brachial indices. To the extent that distal element elongation carries this significance among lemurs, the low brachial index of *Hadropithecus* suggests less cursoriality than in *Archaeolemur*.

The argument that humeral gracility signals cursoriality is weak. Humeral gracility correlates poorly with cursoriality among anthropoids; certainly cursorial cercopithecids cannot easily be distinguished from non-cursorial cercopithecids on the basis of the gracility of their humeral shafts (Table 3). It also correlates only weakly with femoral gracility among cercopithecids. Furthermore, the humerus of *Hadropithecus* is not very gracile. Its robusticity index (or mid-shaft transverse diameter \times 100/maximum length = 8.0) lies at the high rather than the low end of the species mean range for cercopithecids (Table 3). Mean values for humeral robusticity in *Archaeolemur majori* (8.9) and *Archaeolemur edwardsi* (9.8) are even higher.

TABLE 3. Forelimb indices for the *Archaeolemuridae* and selected anthropoids

Taxon	Brachial index	Humeral robusticity index
<i>Archaeolemur majori</i>	104 ¹	8.9 (13)
<i>Archaeolemur edwardsi</i>	105 ¹	9.8 (18)
<i>Hadropithecus stenognathus</i>	84 ²	8.0 (3)
<i>Theropithecus gelada</i>	108 (10)	6.3 (2)
<i>Papio hamadryas/anubis</i>	109 (22)	7.1 (19)
<i>Erythrocebus patas</i>	107 (12)	7.8 (14)
<i>Mandrillus sphinx</i>	109 (6)	7.2 (4)
<i>Cercopithecus aethiops</i>	98 (12)	7.2 (18)
<i>Macaca fascicularis</i>	97 (29)	7.3 (26)
<i>Nasalis larvatus</i>	105 (15)	6.1 (9)
<i>Presbytis cristata</i>	95 (12)	7.2 (9)
<i>P. rubicunda</i>	113 (12)	6.5 (7)
<i>Alouatta palliata</i>	89 (3)	7.3 (7)
<i>A. seniculus</i>	92 (8)	6.4 (11)
<i>Pithecia pithecia</i>	93 (10)	5.9 (8)
<i>Pan troglodytes</i>	92 (39)	7.6 (4)
<i>Gorilla gorilla</i>	80 (27)	7.8 (4)
<i>Pongo pygmaeus</i>	101 (33)	6.0 (11)

Mean values are represented. Numbers in parentheses represent individuals in the sample.

Brachial index = (radial length \times 100)/(humeral length).

Humeral robusticity index = (humeral midshaft transverse diameter \times 100)/(humeral length).

¹ Associations for giant subfossil lemur postcranial specimens collected in the early 1900s have been largely lost. Therefore, subfossil lemur brachial indices cannot be calculated with certainty. Individual associations, when known, are used; index values are also estimated from site means.

² The value for *Hadropithecus* is based on an apparent association of forelimb specimens from Tsirave.

In comparison to most cercopithecids, *Archaeolemur* has relatively short and robust humeri. The humerus of *Hadropithecus* is marginally more similar to Old World monkeys in this respect.

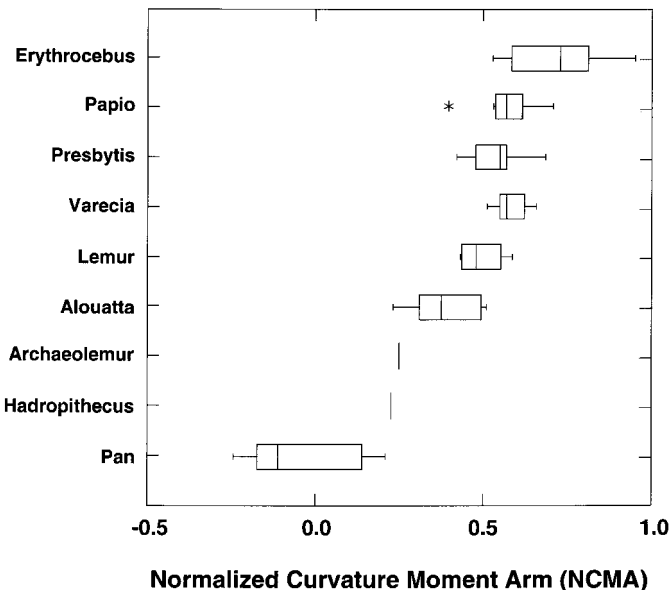
One of the strongest signals of terrestrial cursoriality is retroflexion of the humeral shaft (Preuschoft, 1973; Richmond, 1995). It has been suggested that long bone curvature directly reflects dynamic forces experienced in the growing animal (Lanyon, 1980; Lanyon and Rubin, 1985). Among anthropoids at least, the degree of anteroposterior curvature of the humerus appears to be related to locomotor mode. Many authors have noted that suspensory and climbing apes have straight humeral shafts whereas more quadrupedal species possess humeri that curve anteriorly (or "retroflex") in the region of the deltoid insertion (Napier and Davis, 1959; Hill, 1962; Andrews and Groves, 1976; Swartz, 1990). Humeral shaft curvature has been used to assess locomotor behavior in various fossil anthropoids (Napier and Davis, 1959; Fleagle and Simons, 1982;

Rose, 1989, 1993; Pilbeam et al., 1990; Moya-Sola and Kohler, 1996).

To assess the degree of anteroposterior curvature of humeral shafts, we measured normalized curvature moment arms (NCMA) following Swartz (1990; see also Biewener, 1983; Stern et al., 1995). Of a number of possible measures of curvature, this is probably the most biomechanically meaningful for the humerus. NCMA is defined as the maximum distance (or moment arm) from the central axis of the shaft to a line connecting the proximal and distal cortices; it is made "scale-free" by dividing by the midshaft diameter (Swartz, 1990). Data were digitized (using the MacMorph morphometric data acquisition package of Spencer and Spencer, 1995) from lateral view video images of casts of humeri of *Hadropithecus* and *Archaeolemur* and a comparative sample of 70 humeri of extant lemurs and anthropoids. The non-hominoid primate sample includes arboreal as well as terrestrial quadrupeds; their humeri are considerably more curved than those of chimpanzees. Although chimpanzees have specialized secondary quadrupedal adaptations (Tuttle, 1967, 1970), they use their forelimbs in quadrupedalism very differently from other primates (Inouye, 1992; Larson, 1993). They also engage in considerable climbing and suspension (Hunt, 1992; Doran, 1993), especially when young (Doran, 1992). The straightness of their humeral shafts is consistent with that observed in other apes (Richmond, 1995) and contrasts strongly with the highly retroflexed shafts of *Papio* and *Erythrocebus patas*. Terrestrial cercopithecoids, such as baboons and especially patas monkeys, are specialized behaviorally and anatomically in their adaptations for high speed ground locomotion (Hall, 1968a,b; Rose, 1977). Their exceptionally curved humeri presumably develop in response to the unique mechanical loads experienced during such rapid quadrupedalism.

Figures 3 and 4 display the humeral shaft curvature of *Archaeolemur* and *Hadropithecus*, compared to that of other lemurs and anthropoid primates. Humeral shaft curvature in both *Archaeolemur* and *Hadropithecus* is intermediate between that of chimpanzees on the one hand and all of the

Fig. 3. Boxplot showing humeral shaft curvature in (top to bottom): *Erythrocebus patas* (n = 20); *Papio hamadryas* (n = 9); *Presbytis* spp. (*melalophus*, *obscura*, and *rubicunda*) (n = 10); *Varecia variegata* (n = 7); *Lemur catta* (n = 4); *Alouatta seniculus* (n = 10); *Archaeolemur majori* (n = 1); *Hadropithecus stenognathus* (n = 1); and *Pan troglodytes* (n = 10). Each box represents the interquartile range; the inner vertical lines mark the medians. The whiskers show the most extreme observed values within ± 1.5 interquartile ranges of the outer edges of the box. Asterisks represent outliers.



quadrupedal primates in our sample on the other. The greater humeral curvature in these subfossil taxa compared to chimpanzees is consistent with their reconstructions as non-suspensory quadrupeds (Walker, 1974; Jungers, 1980; Godfrey, 1988; Godfrey et al., 1995). However, in contrast to those of terrestrial Old World monkeys, agile arboreal quadrupedal lemurs (such as *Varecia*), and semiterrestrial quadrupedal lemurs (such as *Lemur catta*), the humeri of *Archaeolemur* and *Hadropithecus* are remarkably straight. This evidence indicates that these subfossil taxa were not agile quadrupeds, and, in particular, that they did not practice the specialized cursorial, terrestrial locomotion of species such as baboons and patas monkeys (also cf. Jungers, 1980; Godfrey et al., 1995). A similar case could be made on the basis of mediolateral curvature of the humeral shaft (Pilbeam et al., 1990; Moya-Sola and Kohler, 1996), which is lacking in *Archaeolemur* and *Hadropithecus* and marked in quadrupedal cursorial monkeys.

In summary, the allocation of gracile archaeolemurid hindlimb bones to *Hadropithecus* cannot be justified on functional grounds. Taken alone, the forelimb bones of *Hadropithecus stenognathus* do not support the hypothesis that *Hadropithecus* was a terrestrial cursor. Nothing about the hindlimb

bones that Lamberton ascribed to *Hadropithecus stenognathus* allies these specimens with known forelimb bones of this species. Instead, Lamberton's allocations yield contradictory functional signals and aberrant estimates of body mass.

If Lamberton did misidentify the hindlimb bones of *Hadropithecus*, then unrecognized hindlimb specimens of *Hadropithecus* may exist in collections of subfossil lemurs. We believe that this is the case. Museum collections in Europe and Madagascar house some specimens that are clearly archaeolemurid in morphology, yet they fall well outside the size ranges of samples of *Archaeolemur* from the same sites. Furthermore, all of these specimens come from sites that have yielded skulls, mandibles, and forelimb bones of *Hadropithecus* (Table 4); the distribution of these sites is shown in Figure 5. In the next section, we review these materials and discuss their prior attributions.

NEW ALLOCATIONS FOR HADROPITHECUS

Calcaneus from Andrahomana

Walker (1967) identified a calcaneus from Andrahomana in the collections of the British Museum [Natural History] as belonging to *Megaladapis madagascariensis*. As noted

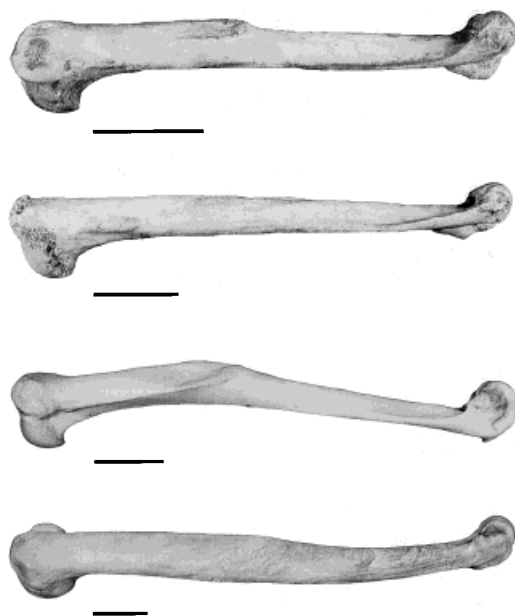


Fig. 4. Lateral views of humeri of, from top to bottom, *Archaeolemur*, *Hadropithecus*, *Papio*, and *Pan*. Compare the anteriorly convex curvature (=retroflexion) in *Papio* to the straight shafts of *Archaeolemur*, *Hadropithecus*, and *Pan*. The *Pan* humerus shown here curves slightly in the opposite direction, represented by a "negative" curvature in Figure 3. Scale bars are 3 cm.

above, recent discoveries of associated foot bones of *Megaladapis* prove that this identification is incorrect (Wunderlich et al., 1996). The calcaneus, BMNH M7946, is similar in morphology and proportions yet much larger in size than those known for *Archaeolemur* (Fig. 6a); it is very different in morphology from that of *Megaladapis* (Fig. 6b). It is broken laterally along its proximal half and proximomedially at the calcaneal tuberosity and just distal to it. The calcaneal tuberosity is therefore only partially complete.

The size of the calcaneus greatly exceeds that of specimens of *Archaeolemur majori* and *A. edwardsi* (Fig. 7). This is of particular interest because the specimen comes from Andrahomana, a site which has yielded the smallest known calcaneus of *Archaeolemur majori* (BMNH M7945; see Fig. 6a). An even smaller calcaneus from Andrahomana (BMNH M7089) was identified by Walker (1967) as belonging to *Archaeolemur*; however, this specimen actually belongs to *Pachylemur* (Godfrey, 1977).

M7946 is a broad, blocky, and robust calcaneus. The plantar surface is broad and

TABLE 4. Geographic distributions of all specimens of *Archaeolemur*, forelimb and craniodental specimens of *Hadropithecus* (labeled "Hadropithecus"), and problematic robust hindlimb specimens (labeled "?")

Ambararata	<i>Archaeolemur</i>
Ambolisatra	<i>Archaeolemur</i>
Ambovombe ¹	<i>Hadropithecus</i>
Amparihingidro	<i>Archaeolemur</i>
Ampasambazimba ²	<i>Archaeolemur</i> , <i>Hadropithecus</i> , (?)
Ampoza-Ankazoabo ³	<i>Archaeolemur</i> , <i>Hadropithecus</i>
Anavoha	<i>Archaeolemur</i> , <i>Hadropithecus</i> , (?)
Andrahomana	<i>Archaeolemur</i> , <i>Hadropithecus</i> , (?)
Ankarana ⁴	<i>Archaeolemur</i>
Ankilitelo	<i>Archaeolemur</i>
Anjohibe	<i>Archaeolemur</i>
Anjohikely	<i>Archaeolemur</i>
Antsirabe	<i>Archaeolemur</i>
Antsiranana	<i>Archaeolemur</i>
Beavoha	see Bevoha
Behavoha	see Bevoha
Belo	<i>Archaeolemur</i> , <i>Hadropithecus</i> , (?)
Beloha	see Anavoha
Bemafandry	<i>Archaeolemur</i>
Betafo	see Morarano
Betioky-Tulear ⁵	see Taolambiby
Bevoha	<i>Archaeolemur</i>
Itampolobe ⁶	<i>Archaeolemur</i>
Lamboharana	<i>Archaeolemur</i>
Manombo-Tulear ⁵	see Ambolisatra
Masinandraina	<i>Archaeolemur</i>
Morarano-Betafo	<i>Archaeolemur</i>
Nosy Ve	<i>Archaeolemur</i>
Sambaina	<i>Archaeolemur</i>
Taolambiby	<i>Archaeolemur</i>
Tsiandroina	<i>Archaeolemur</i>
Tsirave	<i>Archaeolemur</i> , <i>Hadropithecus</i>

¹ Six partial mandibles of *Hadropithecus stenognathus* were collected by Decary and accessioned by the Institut de Paléontologie, Paris, in 1924 and 1925. The only provenience information is "Ambovombe"—a city in the extreme south of Madagascar. It is located between Andrahomana in southeastern Madagascar and the Lower Menarandra sites (Anavoha, Beavoha, Bemafandry, Itampolo, and Lamboharana) in southwestern Madagascar.

² Several of the robust femora appear to have belonged to the Standing collection. Standing excavated numerous specimens at Ampasambazimba. Many of the bones in the Standing collection have no marked provenience.

³ Accessioned by the Institut de Paléontologie in 1910, materials collected by Barféty-Bührer, including a mandible, maxilla, and humerus of *Hadropithecus*, are listed as coming from Morondava. Morondava is a city on the west coast of Madagascar, considerably north of Toliara; the specimens may come from the nearby fossil site Ampoza-Ankazoabo. Carleton (1937) illustrates this humerus as having come from Ampoza-Ankazoabo. Other sites in the vicinity of Morondava are Belo, Tsirave, and Ambararata. Specimens of *Hadropithecus* have been found at Belo and Tsirave.

⁴ Ankarana is an uplifted block of Jurassic limestone in northern Madagascar that contains several cave systems; all have yielded specimens of *Archaeolemur* (Simons et al., 1990). Caves that have yielded abundant *Archaeolemur* include Antsiranandoha, Andrafiabe, and the Cave of the Lone Barefoot Stranger (Fitsangatsanganan' Ilay Olona Tokana).

⁵ Some archaeolemurid specimens in the collections of the Académie Malgache are recorded as coming from "Betioky-Tulear" and "Manombo-Tulear." Manombo and Betioky are villages in the vicinity of Toliara (= Tulear). The sites Ambolisatra and Andranovato are very near Manombo (see Lamberton, 1934, 1937; Battistini, 1971a), and specimens labeled "Manombo-Tulear" may actually come from one of these sites. The subfossil-bearing site of Taolambiby is very near Betioky (Raisin and Verin, 1967; Battistini, 1971b), and specimens labeled "Betioky-Tulear" may actually come from Taolambiby. Several femora from Manombo-Tulear were attributed by Vuillaume-Randriamanantena to *Hadropithecus*, based on their close match to Lamberton's misallocated Tsirave specimen. No craniodental or forelimb specimens of *Hadropithecus* have been found at Ambolisatra or Taolambiby. In our judgment, all of the femora from "Manombo-Tulear" are *Archaeolemur*.

⁶ This site should not be confused with Itampolo; see Tattersall (1987).

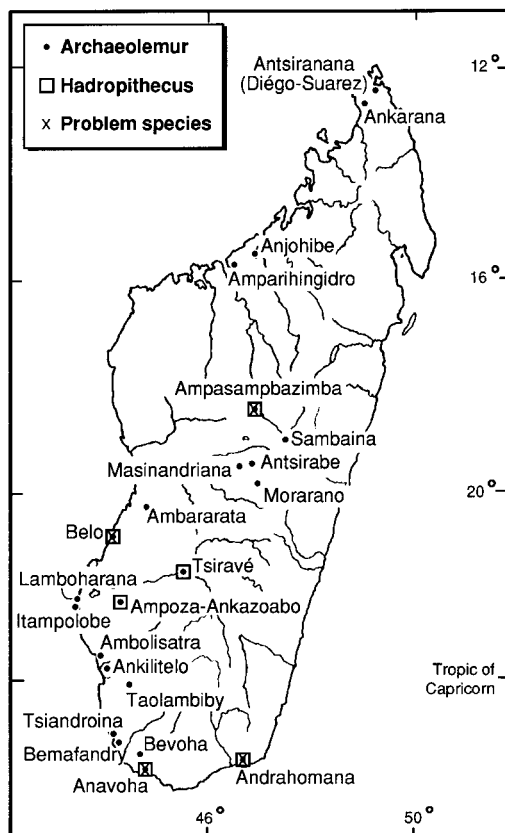


Fig. 5. Geographic distributions of *Archaeolemur* (all specimens); *Hadropithecus* (cranial and forelimb specimens); and large archaeolemurid hindlimb specimens. Note the coincidence of the distributions of the problematic hindlimb specimens and the cranial/forelimb specimens of *Hadropithecus*.

flat, resembling *Archaeolemur*. In proportions, the calcaneus is also remarkably similar to that of *Archaeolemur*; the anterior calcaneus is short, and the posterior calcaneus is expanded in length and broad at the heel. From proximal view, the calcaneal tuberosity is triangular to rectangular in shape, broad plantarly and flat proximally, exhibiting none of the medial or plantar elongation present in *Megaladapis* or *Palaeopropithecus*, respectively.

The proximal facet for the talus is large, flat, and oval in shape. Its articular surface faces superiorly. It differs considerably from the more curved proximal facet of *Archaeolemur*: In the latter taxon, the distal portion of the proximal facet faces anteriorly to anterolaterally while the proximal portion faces

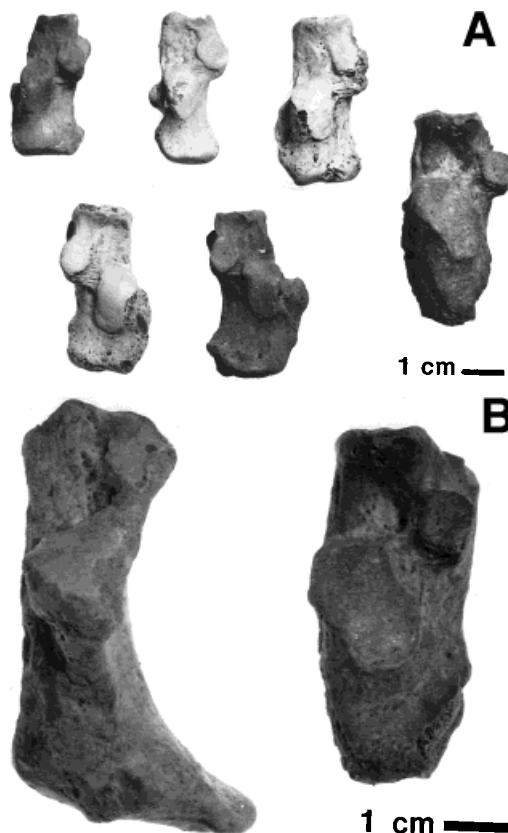


Fig. 6. **a:** From upper left, clockwise, calcanei of: *Archaeolemur majori* (BMNH M7945 from Andrahomana); *A. sp. (cf. edwardsi)* (UALPV 87-263 from Ankarana); *A. sp. (cf. edwardsi)* (Duke University Primate Center 11837 left side, from Ankarana); *Hadropithecus stenognathus* (BMNH M7946, from Andrahomana, our allocation); *A. sp. (cf. edwardsi)* (USNM 447012/UALPV uncatalogued, from Anjoihikely); *A. sp. (cf. edwardsi)* (DUPC 11837 right side, from Ankarana). **b:** Comparison of calcanei of (left) *Megaladapis* (DUPC 7950 from Ankarana) and (right) BMNH M7946 from Andrahomana. BMNH M7946 is archaeolemurid and not megaladapid in morphology.

posteromedially. In BMNH M7946, the proximal facet is very flat, and all portions of its face superiorly except the most distal portion which faces slightly anterolaterally.

The distal (sustentacular) facet for the talus is strongly waisted and almost completely divided into a distal and a proximal portion as occurs frequently in *Archaeolemur* as well as in many New and Old World monkeys (Langdon, 1986; Rose, 1986; Strasser, 1988). The proximal portion of this facet is large and round; the distal portion is teardrop-shaped. Both portions of the facet

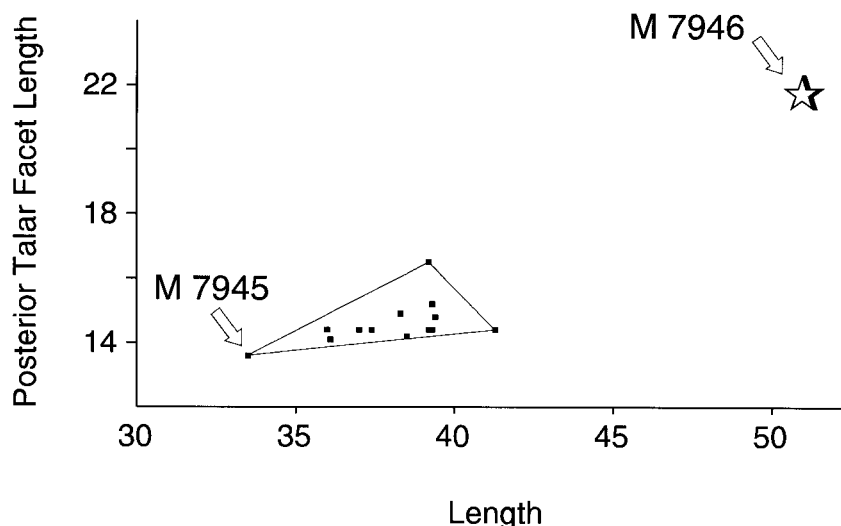


Fig. 7. Posterior talar facet length (Y) vs. total calcaneal length (X) of *Archaeolemur* (closed squares) and *Hadropithecus* (BMNH M7946, open star, our allocation). BMNH M7946 comes from Andrahomana, a site which has also yielded some of the smallest specimens of *Archaeolemur* (e.g., BMNH M7945). Measurements in mm.

are flat, although the posterior portion sits at an angle to the calcaneal body such that the articular surface faces distolaterally. Together, the articular facets for the talus are indicative of a subtalar joint with limited mobility.

The facet for the cuboid is crescentic in shape and pitted medially. This probably provided articulation for a cuboid pivot, suggesting substantial mobility at this joint. The pivot, however, is not as deep as that seen in some other extinct indroids (i.e., *Babakotia* and *Mesopropithecus*) that have a nearly "ball-and-socket" type of joint (Wunderlich et al., 1994). The joint was therefore probably less mobile than in these highly suspensory forms. There is a tubercle, slightly damaged, medial to the facet for the cuboid, which forms the base of the flexor fibularis groove. The groove for flexor fibularis longus is not deep, although the sustentaculum tali projects far medially.

Although it is partially broken off, there was clearly a large tubercle on the lateral side of the calcaneus (Walker, 1967). The tubercle is positioned along the plantar border of the lateral calcaneus, midway along the length of the bone and plantar to the middle of the proximal facet for the talus. It

resembles the lateral tubercle of *Archaeolemur* (Lamberton, 1939; Decker and Szalay, 1974), although it is unclear (because of the breakage) whether a ridge extended posteriorly to the calcaneal tuberosity as frequently occurs in specimens of *Archaeolemur*. When present in extant prosimians, the lateral (peroneal) tubercle is small, longer superoinferiorly and much less laterally projecting than that of the archaeolemurids. Extant anthropoids frequently have a large peroneal tubercle that projects laterally and can extend proximally to the calcaneal tuberosity as a bony ridge. In Old World monkeys, this tubercle serves as the attachment site for the peroneal retinaculum and as the site of origin of the quadratus plantae muscle, a muscle that is "consistently absent in prosimians" (Howell and Straus, 1933, p. 172); it can also give some origin to one of the abductors of the fifth digit. Decker and Szalay (1974) discuss the tubercle of *Archaeolemur* and claim that it not a true peroneal tubercle (which they associate with the distally placed peroneal tubercle of non-primate mammals, which projects laterally, separating the peroneal tendons and serving as a trochlea for the peroneus longus tendon). They, like Lamberton (1939), assert

that this tubercle in both *Archaeolemur* and extant prosimians serves as the attachment site for the calcaneofibular and talocalcaneal ligaments. In fact, the small lateral tubercle of extant prosimians is situated well anterior to the attachment site for the calcaneofibular and talocalcaneal ligaments. It actually serves as the attachment for the peroneal retinaculum, and the abductor ossis metatarsi muscle may take the proximal part of its arc-shaped origin from this tubercle. The large lateral tubercle on BMNH M7946, therefore, was probably indicative of a large peroneal musculature but may also suggest a substantial origin for the abductor ossis metatarsi muscle.

The robust calcaneus suggests a species with a strong weight-bearing foot which compromised mobility for stability at the subtalar joint yet retained the capacity for considerable transverse tarsal mobility. A strong peroneal mechanism, implied by the large lateral tubercle, suggests strength in eversion and potentially in hallucal grasping. Eversion is important during the stance phase of arboreal and terrestrial quadrupedalism in monkeys to transfer weight toward the medial side of the foot, especially when the foot is in a toed-out position (Stern and Susman, 1983; pers. obs. REW). The function of the abductor ossis metatarsi is as yet unclear, although it has been suggested that this muscle serves to laterally deviate the forefoot when positioning it on an arboreal support (Gebo, 1986).

Os coxae from Andrahomana

The Vienna Naturhistorisches Museum has in its collections portions of a large but very partial pelvis from Andrahomana (VNM 1934.IV.48a and b; Fig. 8). This pelvis is strikingly larger than other archaeolemurid pelvises from Andrahomana, and may belong to *Hadropithecus*. Because so little of the pelvis is present, it is impossible to tell the degree of overall size difference between this pelvis and those of *Archaeolemur*. Only the right and left acetabulae and parts of the right and left pubic and ischial rami are preserved. Whereas we believe that VNM 1934.IV.48a and b do belong to *Hadropithecus*, these fragments are sufficiently close in morphology to *Archaeolemur edwardsi* that

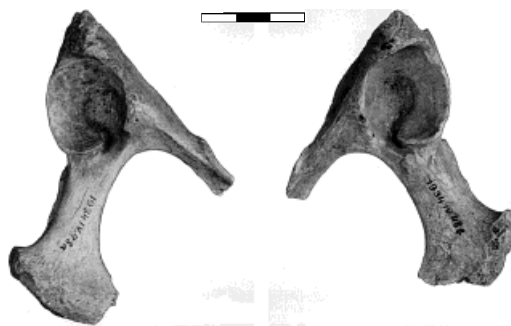


Fig. 8. Portions of a pelvis (VNM 1934.IV.48a and b) of a large archaeolemurid from Andrahomana. Possibly *Hadropithecus* (our allocation). Scale is 1 cm.

it is impossible to make this allocation with complete confidence. The preserved fragments are only marginally larger than comparable portions of pelvises of *Archaeolemur edwardsi* from central and northern Madagascar. The tremendous size disparity exhibited by archaeolemurid calcanei from Andrahomana is not repeated here. Furthermore, whereas Andrahomana was home to some of the smallest *A. majori*, there are a few fragmentary dental and forelimb specimens of a large *Archaeolemur* from Andrahomana in the collections of the BMNH and the VNM. This suggests that the geographic range of *A. edwardsi* may have, at least intermittently, reached the region of Fort Dauphin (perhaps through the corridor of the eastern rainforest). We cannot rule out the possibility that this pelvis belonged to a large *A. edwardsi*.

The acetabulae of VNM 1934.IV.48a and b are deep and moderately large (the diameter measured perpendicular to the acetabular notch is over 28 mm); they are large enough to accommodate the head of a femur comparable to that from *Belo* described below. There is a rugose surface (part of the anterior inferior iliac spine for the origin of *m. rectus femoris*) just cranial to the acetabulum; however, due to breakage, it is impossible to reconstruct the extent of its development. The lunate surface is asymmetrical, and the anterior, dorsal rim of the acetabulum is slightly thicker than the ventral rim. The ischium is greatly distally (but little dorsally) elongated, thereby increasing the mechanical advantage of the hamstrings for

extending the hindlimb from a pronograde position. The ischial tuberosity is rugose and wide dorsally, the superior pubic ramus relatively narrow, and the obturator crest well demarcated. This morphology supports an inference of dominant quadrupedalism (see Fleagle and Anapol, 1992; Fleagle and Simons, 1995).

Femora from Anavoha, Belo, and Ampasambazimba (?)

Femora A1 through A6 in the collections of the UALPV are from Anavoha (near the town of Beloha, in the Lower Menarandra River Basin, southwest Madagascar); A7 and A8 are of unknown provenience.⁸ Not one of the eight femora in the collections of the Laboratoire de Paléontologie des Vertébrés is whole, and not one preserves the femoral trochlea or condyles. Only one (A1) preserves the head and neck, although the greater trochanter is broken off. One partial shaft (A5) appears to have belonged to a juvenile. These femora are *archaeolemurid* in morphology but massive (Table 5, Fig. 9). They belonged to a species that was significantly heavier than *Archaeolemur majori*.

As noted in the introduction, the Paris collection contains a robust femur from Belo that was originally figured by Grandidier (1905) as "*Palaeopropithecus ingens*" and then by Carleton (1936) as "*Bradylemur robustus*," as well as a second robust shaft (lacking provenience information) with no proximal or distal epiphyses. The midshaft diameters of these specimens match those of femora A1–A8 in the collections of the UALPV, and fall outside the range for *Archaeolemur*. The Belo specimen is the only nearly whole femur of this type (Fig. 10); it is nearly as long as the longest *A. edwardsi* but different in morphology. The shaft is damaged, and the medial and lateral lips of the patellar groove are worn.

The femur differs from *Archaeolemur* in exhibiting extreme anteroposterior compression of the diaphysis and unusual flattening of the posterior face of the shaft. The shaft is very straight in sagittal view, and exhibits slight mediolateral curvature (convex medi-

TABLE 5. Comparisons of femoral dimensions (in mm) of *Archaeolemur* and *Hadropithecus* (new allocations)

	n	Min	Max	Mean	Standard error
<i>t</i> -tests femoral mid-shaft transverse diameter at two sites					
<i>Archaeolemur</i>	21	15.1	19.5	18.3	0.262
<i>Hadropithecus</i>	2	24.4	24.6	24.5	0.1
<i>t</i> -test: df = 21, <i>t</i> = -7.20, <i>P</i> < .001					
Anavoha					
<i>Archaeolemur</i>	29	13.9	17.6	15.8	0.173
<i>Hadropithecus</i>	5	21.1	23.3	22.2	0.419
<i>t</i> -test: df = 32, <i>t</i> = -14.23, <i>P</i> < .001					
<i>t</i> -test femoral mid-shaft transverse diameter at all sites					
<i>Archaeolemur</i>	116	13.9	20.9	16.9	0.158
<i>Hadropithecus</i>	9	21.1	24.6	22.9	0.418
<i>t</i> -test: df = 123, <i>t</i> = -10.24, <i>P</i> < .001					

ally) in anterior view. The posterior face of the shaft is smooth; muscle markings for the adductors and for gluteus superficialis are faint or nonexistent. On the anterior face, the intertrochanteric line for the insertion of the iliofemoral ligament is equally faint. Femoral shafts of *Archaeolemur* are less robust; they tend to be straight in both frontal and sagittal planes, although some of the more gracile specimens exhibit slight anteroposterior curvature (convex anteriorly). The linea aspera on the posterior face of the shaft is usually distinct, as is the intertrochanteric line on the anterior face of the shaft.

The tip of the greater trochanter of the Belo femur greatly surpasses the femoral head. As in *Archaeolemur*, there is little anterior overhang of the proximal border of the greater trochanter. The obturator fossa is deep and long, and the femoral neck is constricted just lateral to the head, as in *Archaeolemur*. The femoral head is relatively small (though nevertheless larger in absolute size than in *Archaeolemur*); it does not bear the posterior extension onto the neck that is typical of *Archaeolemur*. The flattened area on the posterior face of the shaft for insertion of m. quadratus femoris is relatively larger than in *Archaeolemur*; be-

⁸These specimens apparently belonged to the Standing collection. H.F. Standing did not mark the site on many of the specimens found at Ampasambazimba during the early 1900s.

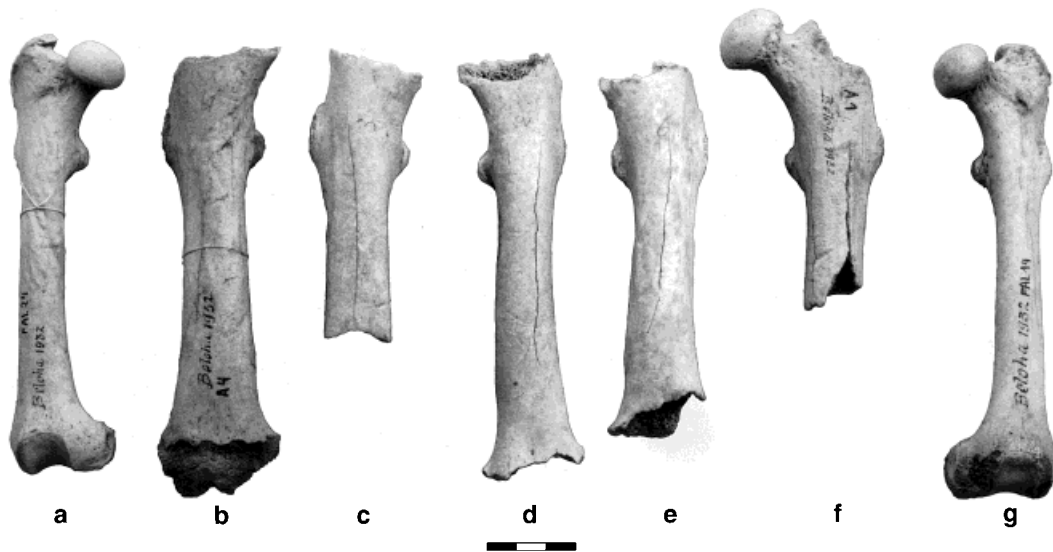


Fig. 9. Whole femora of *Archaeolemur* and femoral shafts of *Hadropithecus* (our allocations) from Beloha Anavoha (southwestern Madagascar). All specimens in the collections of the UALPV, from left to right: (a) FAL24, right femur of *Archaeolemur majori*; (b,c) right femora of *Hadropithecus*, specimens A4 and A3; (d-f) left femora of *Hadropithecus*, specimens A2, A6, and A1; (g) FAL14, left femur of *Archaeolemur majori*.

cause the lesser and third trochanters are very distally situated on the shaft. The distance from the tip of the greater trochanter to the distal margin of the third trochanter on the Belo femur is 40% of the total length of the shaft; this compares to a mean of 32.8% and a range of 28.8 to 35.4% for a sample of 31 *Archaeolemur* specimens.

The distal femur is unique among archaeolemurids in bearing a depression on the proximal articular margin of the medial condyle for the fabella (sesamoid) of the tendon of origin of the medial head of gastrocnemius. The femoral condyles are slightly more anteroposteriorly compressed than is typical for *Archaeolemur*. The biepicondylar breadth is enormous, and the medial femoral condyle is significantly wider than the lateral.

The femur suggests a species that was predominantly quadrupedal but neither agile nor cursorial. Robust and anteroposteriorly compressed femoral shafts are uncharacteristic of agile quadrupeds (Table 6). Across primate families, there is a tendency for more agile forms (particularly leapers) to have slender femoral shafts, and for slower

and more quadrupedal climbers to have wider, flatter, and more robust femoral shafts (Ruff and Runestad, 1992; Demes and Jungers, 1993a). Cercopithecids have a narrow range of variation in this regard; none matches the robusticity of any archaeolemurid. Within the Cercopithecidae, the leaping colobines tend to have more slender, less anteroposteriorly compressed femoral shafts than do cercopithecines (particularly papionins). The same contrast holds for galagonids (where smaller-bodied leapers such as *Galago senegalensis* have more slender and less compressed femora than larger-bodied quadrupedal climbers such as *Otolemur crassicaudatus*); atelids (where leapers such as *Pithecia* have more slender femora than deliberate quadrupedal climbers such as *Alouatta*); and Malagasy lemurs (where specialized leapers such as *Indri* and *Propithecus* have the lowest femoral robusticities and the least anteroposteriorly compressed shafts, more quadrupedal lemurs have intermediate values, and slow climbing megaladapids and quadrupedal hangers such as *Palaeopropithecus* have very high femoral robusticities and extremely flat-

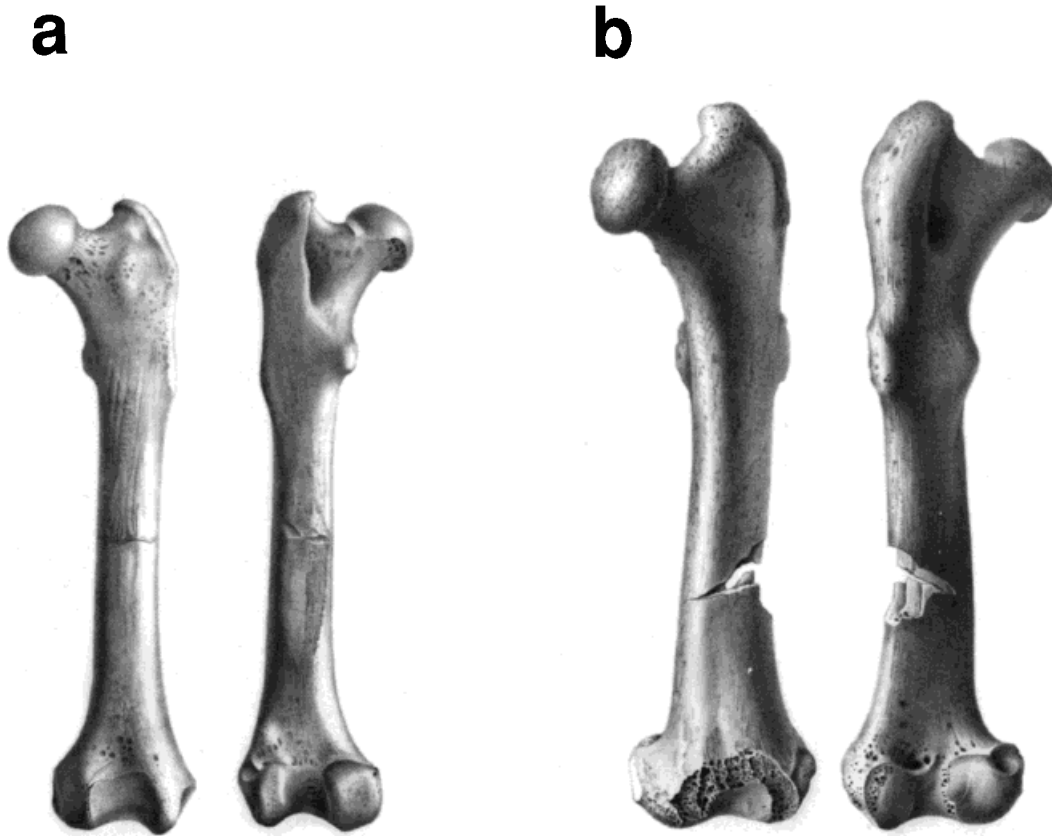


Fig. 10. Right femur of *Archaeolemur majori* (a) and left femur of *Hadropithecus stenognathus* (b) (our allocation) from Belo (western Madagascar), in the collections of the Muséum Nationale d'Histoire Naturelle, Paris. Reproduced to scale from Plates 9 and 12 of Grandidier (1905). The right femur of *Archaeolemur* is shown in mirror image to facilitate comparison with the left femur of *Hadropithecus*. For scale, the latter is 183.5 mm from the tip of the greater trochanter to the lateral condyle.

tened femoral midshafts). Among the Hominoidea, chimpanzees and (particularly) gibbons have more slender and less anteroposteriorly compressed femora than do gorillas and orangutans.

*Archaeolemur*id femora rival those of gorillas and orangutans in robusticity and midshaft compression. They are less robust and anteroposteriorly compressed than those of megaladapids and some palaeopropithecids but far more so than those of lemurids and (especially) indrids. Robusticity and midshaft compression are significantly greater in the problematic specimens from Anavoha, Belo, and Ampasambazimba than in any *Archaeolemur* species (Table 6).

Figure 11 compares the femoral dimensions of these specimens (our *Hadropithecus*, open stars) with *Archaeolemur* species (closed squares) and Lamberton's "*Hadropithecus*" (open squares). The distinctiveness of our *Hadropithecus* (and the similarity of Lamberton's "*Hadropithecus*" to *Archaeolemur*) is obvious. Figure 11b shows midshaft dimensions of femora from Anavoha only. When controlled for geography, the separation of robust from gracile *archaeolemur*id specimens is clearer still. This pattern of differentiation parallels that of the skulls and forelimbs of *Hadropithecus* and *Archaeolemur*. All of this evidence supports the conclusion that Lamberton erred in his hind-

TABLE 6. Comparisons of femoral indices of *Archaeolemur*, *Hadropithecus* (new allocations) and other primates using one-way ANOVA

	Femoral midshaft compression index ¹		Femoral robusticity index ²	
	n	Mean (SD)	n	Mean (SD)
One-way ANOVA by species, Archaeolemuridae only				
<i>Archaeolemur majori</i>	62	84.0 (5.0)	39	9.7 (0.6)
<i>A. edwardsi</i>	54	83.1 (4.9)	28	10.2 (0.6)
<i>Hadropithecus stenognathus</i>	9	70.8 (4.5)	1	12.0 —
All	125	82.6 (5.9)	68	9.9 (0.7)
	F = 28.4 (df 2, 122) <i>P</i> < .001		F = 11.2 (df 2, 65) <i>P</i> < .001	
One-way ANOVAs by family for femoral midshaft A-P compression and femoral robusticity in 63 primate species (587 individuals) in nine families. Family means are averages of species means				
Indridae	5	107.8 (5.6)	5	4.8 (0.2)
Galagonidae	2	100.9 (6.1)	2	5.9 (0.4)
Lemuridae	10	101.4 (8.3)	10	6.4 (1.6)
Cercopithecidae	18	97.1 (2.6)	18	6.4 (0.6)
Atelidae	11	90.8 (6.8)	12	6.2 (0.6)
Pongidae	4	85.4 (11.1)	4	8.7 (1.2)
Archaeolemuridae	3	79.3 (7.4)	3	10.6 (1.2)
Palaeopropithecidae	7	75.6 (7.4)	7	11.4 (2.4)
Megaladapidae	2	63.6 (2.3)	2	14.4 (0.03)
All	62	92.5 (12.2)	63	7.4 (2.6)
	F = 21.2 (df 8, 53) <i>P</i> < .001		F = 29.7 (df 8, 54) <i>P</i> < .001	

¹ Midshaft A-P/M-L.² Midshaft M-L/femoral length.

limb allocations for *Hadropithecus*, and that the robust hindlimb bones described above actually belong to *Hadropithecus*.

Bradylemur robustus. In this section, we defend our view that these allocations are incorrect.

SPECIMENS ATTRIBUTED TO *BRADYLEMUR*

Our case would be weakened considerably if it could be shown, based on crania, dentitions, and forelimb specimens, that yet another large-bodied and robust archaeolemurid once lived in southern, western, and central Madagascar. The validity of just such a species, *Bradylemur robustus*, has been periodically defended, most recently and cogently by Vuillaume-Randriamanantena (1982), and previously by Carleton (1936, 1937), and Ekblom (1951). These authors based their assessments in part on the femora that we have ascribed to *Hadropithecus* (i.e., the Belo "*Palaeopropithecus*" and specimens A1–A8 in the Malagasy collections) and also on cranial and forelimb specimens from southern and western Madagascar. Table 7 lists specimens that were accepted by Carleton and by Vuillaume-Randriamanantena (1982) as belonging to

Historical background

Bradylemur was named for a partial mandible (lacking its ascending ramus and central incisors) and a left upper jaw with two premolars and two molars from Belo, west coast of Madagascar (Grandidier, 1899). Grandidier took these specimens to belong to a species that was similar in morphology but larger than *Archaeolemur*: he called it *Bradylemur robustus*. In 1900, Grandidier named several additional archaeolemurids, including *Archaeolemur robustus* based on limb bones from Belo (Grandidier, 1900), and *Bradylemur bastardi* based on specimens collected at the nearby site, Ambolisaotra. Two years later, Grandidier (1902b) sank *B. bastardi* into *A. majori*, and *A. robustus* into *Bradylemur robustus*. Thus, Grandidier (1905) continued to accept a large-bodied archaeolemurid, *Bradylemur robustus*, as distinct from species of *Archaeolemur*; but he rejected *Bradylemur bastardi*.

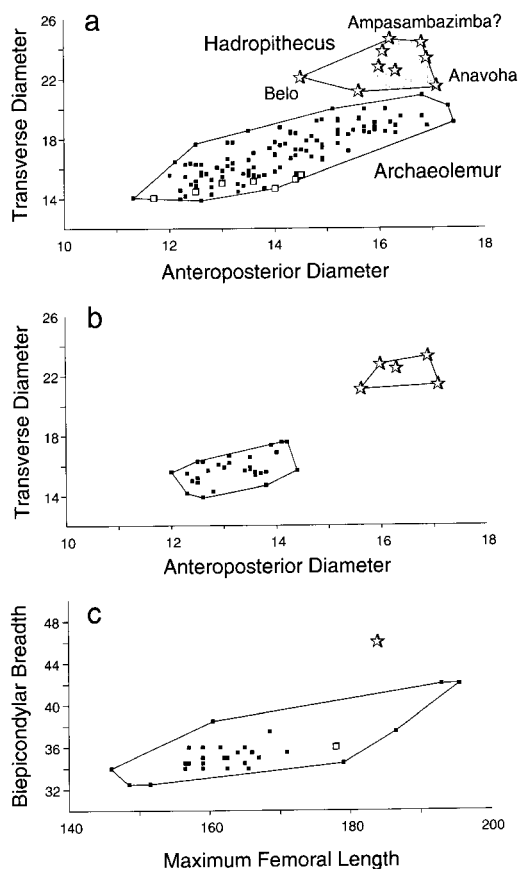


Fig. 11. **a:** Femoral midshaft transverse (Y) vs. midshaft anteroposterior (X) diameter of *Archaeolemur* (solid squares), *Hadropithecus* (our allocations, open stars), and specimens previously allocated to *Hadropithecus* (open squares); all sites. **b:** Same plot, showing specimens from Anavoha only. **c:** Femoral biepicondylar breadth (Y) vs. maximum femur length (X); all sites. *Archaeolemur* (solid squares), our *Hadropithecus* (open star), and prior *Hadropithecus* attribution (open square). All measurements in mm.

Standing (1908) dismissed any independent status for *Bradylemur*. His assessment of *Bradylemur* as a junior synonym of *Archaeolemur* was accepted by Gregory (1915) and Abel (1931), and then by virtually all subsequent authors (e.g., Walker, 1967, 1974; Jolly, 1970; Tattersall, 1973, 1982; Godfrey, 1977, 1988; Jungers, 1980) with the exceptions of Carleton (1936, 1937), Ekblom (1951), and Vuillaume-Randriamanantena (1982).

Carleton (1936, 1937) defended the resurrection of *Bradylemur robustus* based on a

review of postcranial materials in the collections of the BMNH and the MNHN. She regarded a number of specimens as too massive to belong to either *A. majori* or *A. edwardsi*: the femur from Belo that Grandidier (1905) had allocated to *Palaeopropithecus*; the forelimb bones from Belo that Grandidier (1900) had first assigned to *Archaeolemur robustus* and later (1902b, 1905) to *Bradylemur robustus*; and a partial immature skeleton of an archaeolemurid from Ampoza-Ankazoabo that was housed in the BMNH.

Ekblom's (1951) acceptance of *Bradylemur robustus* was based on Carleton (1936). Ekblom allocated to *B. robustus* an ulna from Masinandrana because it seemed to match Carleton's description. When Vuillaume-Randriamanantena (1982) found robust fragmentary archaeolemurid femora in the collections of the Académie Malgache, she too became a defender of *Bradylemur robustus*. Justifiably convinced that these specimens could not belong to either *Archaeolemur majori* or *A. edwardsi*, Vuillaume-Randriamanantena (1982) embraced Carleton's arguments for resurrecting *Bradylemur robustus*.

Cranial materials attributed to *Bradylemur robustus*

The type specimens of *Bradylemur robustus* cannot be distinguished from *Archaeolemur*: They include a partial mandible and maxilla (Grandidier, 1899). Whereas these are the largest jaws of *Archaeolemur* from Belo, they fall well within the size range for this genus. The mesiodistal and buccolingual diameters of the molars fall at the lower end of the range for *Archaeolemur edwardsi* from central Madagascar and at the upper end of the range of variation of *A. majori* from southwestern Madagascar (Figs. 12 and 13). They are among the specimens that have been used to defend a size cline for *Archaeolemur* from southern to central and northern Madagascar (Godfrey and Petto, 1981; Godfrey et al., 1990). Tattersall (1982) attributed these specimens to *A. majori*, whereas Godfrey et al. (1990) and Albrecht et al. (1990) considered them *Archaeolemur* sp. If they actually belong to *A. edwardsi*,

TABLE 7. Species allocations for materials previously attributed to *Bradylemur robustus* (and other misidentified robust archaeolemurid specimens)

Specimen	Site	Carleton	Vuillaume-Randriamanantena	This paper
Grandidier's (1905) type " <i>Bradylemur robustus</i> " maxilla and mandible (Plate 10)	Belo	<i>Bradylemur robustus</i>	<i>Bradylemur robustus</i>	<i>Archaeolemur</i> sp. (cf. <i>edwardsi</i>)
Grandidier's (1905) " <i>Bradylemur robustus</i> " forelimb (Plate 11)	Belo	<i>Bradylemur robustus</i>	<i>Bradylemur robustus</i>	<i>Archaeolemur</i> sp. (cf. <i>edwardsi</i>)
Immature postcranial skeleton (BMNH M13924-13929)	Ampoza-Ankazoabo	<i>Bradylemur robustus</i>	<i>Bradylemur robustus</i>	<i>Archaeolemur</i> sp. (cf. <i>edwardsi</i>)
Ekblom's (1951) " <i>Bradylemur robustus</i> " ulna	Masinandrana	—	—	<i>Archaeolemur</i> sp. (cf. <i>edwardsi</i>)
Filhol's (1895) " <i>Dinolemur grevei</i> " humerus	Belo	—	<i>Bradylemur robustus?</i>	<i>Megaladapis madagascariensis</i>
Grandidier's (1905) " <i>Palaeopropithecus ingens</i> " femur	Belo	<i>Bradylemur robustus</i>	<i>Bradylemur robustus</i>	<i>Hadropithecus stenognathus</i>
UALPV A1-A6 femoral shafts	Anavoha	—	<i>Bradylemur robustus</i>	<i>Hadropithecus stenognathus</i>
UALPV A7-A8 femoral shafts	Ampasambazimba?	—	<i>Bradylemur robustus</i>	<i>Hadropithecus stenognathus</i>
BMNH M7946 Walker's (1967) " <i>Megaladapis madagascariensis</i> " calcaneus	Andrahomana	—	—	<i>Hadropithecus stenognathus</i>
VNM 1934.IV.48a and b Partial pelvis	Andrahomana	—	—	<i>Hadropithecus stenognathus?</i>

then this species ranged from the central highlands of Madagascar all the way to the west coast.

Forelimb materials attributed to *Bradylemur robustus*

Forelimb of "*Bradylemur robustus*" from Belo. The associated humerus, ulna, and radius that Grandidier originally assigned to *Archaeolemur robustus* (Grandidier, 1900), but later (1902b, 1905) transferred to *Bradylemur robustus*, clearly belong to *Archaeolemur*. These specimens are housed at the Paris museum and were figured by Grandidier (1905, Plate 11). They are unusual only in their relatively large size, falling well outside the range of *A. majori* from other sites in the west and from sites in the southwest but within the range of *Archaeolemur edwardsi* from central Madagascar. For example, the humerus is 157 mm long. The lengths of humeri of *A. edwardsi* from Ampasambazimba range from

143 to 164 mm. Humeri of *A. majori* from Anavoha (southwestern Madagascar) range from 126 to 149 mm, and those from Andrahomana (southeastern Madagascar) lie between 123 and 147 mm. Assuming a humero-femoral length index similar to that of other *Archaeolemur* (circa 82–85; see below), the femur of the robust individual from Belo would have been approximately 185–191 mm long—well under the maximum femoral length (194.5 mm) for specimens of *Archaeolemur edwardsi* from Ampasambazimba (see Table 2). Other archaeolemurid long bones from Belo are considerably smaller (Grandidier, 1905), suggesting either that the western *Archaeolemur* was quite variable in body size or that multiple species of *Archaeolemur* coexisted or alternated in the west.

Filhol's "*Dinolemur grevei*" humerus. Vuillaume-Randriamanantena (1982) tentatively assigned to *Bradylemur robustus* an adult

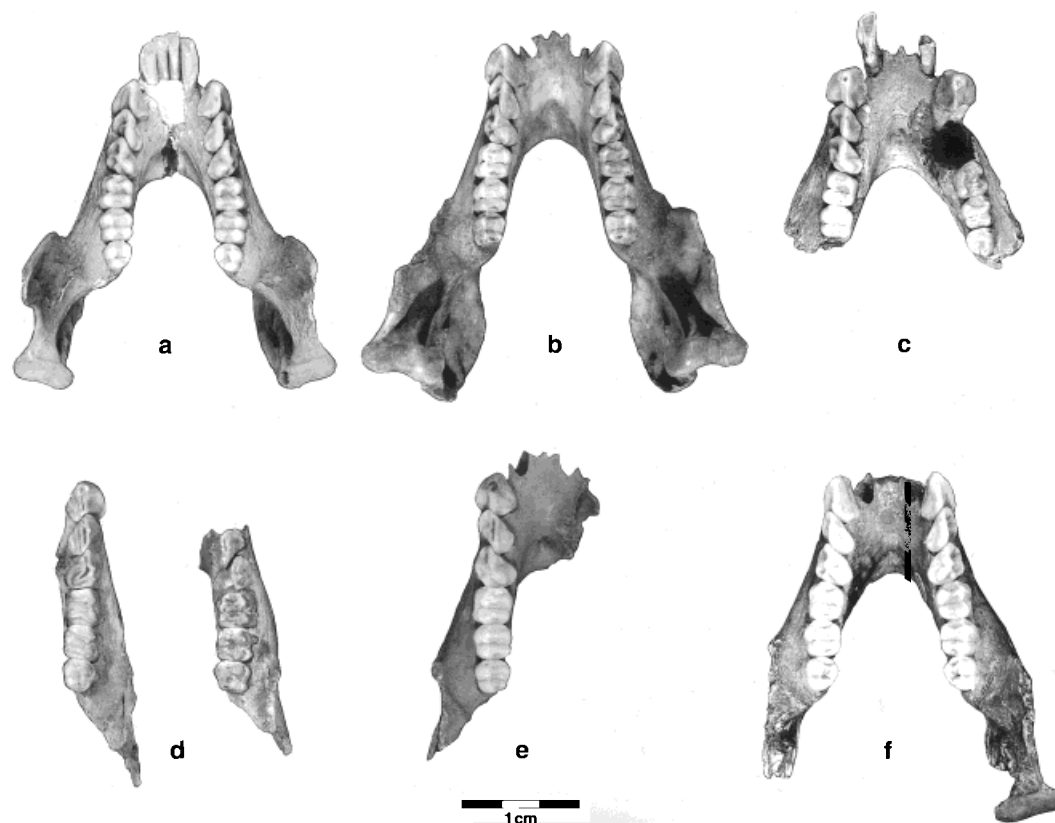


Fig. 12. Mandibles of *Archaeolemur* and “*Bradylemur*.” **a:** *Archaeolemur majori* from southern Madagascar. **b:** *Archaeolemur* sp. (MNHN 1931-6, from Ampoza-Ankazoabo, south central Madagascar). **c:** Type “*Bradylemur robustus*” (MNHN specimen from Belo, west coast). **d:** Additional specimens of *Archaeolemur*

(MNHN type “*Lophiolemur* (= *Archaeolemur*) *edwardsi*” from Belo, west coast). **e:** *Archaeolemur edwardsi* (BMNH M7072 from Antsirabe, central highlands). **f:** *Archaeolemur edwardsi* (BMNH M9911 from Ampasambazimba, central highlands). All photographs printed on the same scale.

humerus that Filhol (1895) had described as “*Dinolemur grevei*” but not figured. According to Filhol, this incomplete humerus displays head dimensions of 36 mm (transverse) and 34 mm (length), plus a length from the summit of the head to the top of the “arcade cubitale” of 161 mm. Filhol’s description is very brief and uninformative; he likens the bone to *Megaladapis*, but then associates it with a distal portion of a femur and a whole calcaneus that he also called *Dinolemur grevei* (and that actually belong to *Archaeolemur*). We have not been able to locate this specimen in the Paris collections. Neither Vuillaume-Randriamanantena nor any subsequent author has examined it directly. The reported dimensions for the head of the humerus match those of *Megaladapis* (*Megal-*

adapis) *madagascariensis*⁹ and well exceed all archaeolemurid species (*Hadropithecus stenognathus*, *Archaeolemur majori* and *A. edwardsi*). Grandidier (1902a) recognized Filhol’s humerus as too large for *Archaeolemur*. Jungers (1976) rejected the attribution of *M. madagascariensis* based on his misreading of the “length” of 161 mm as the total length of the bone, which he regarded as about 20 mm too short. However, given a length of 161 mm from the summit of the head to the top of the “arcade

⁹Filhol (1895) reported values of 36 mm for the transverse diameter of the head of the humerus of “*Dinolemur grevei*” and 34 mm for the anteroposterior length of the head. The means for *Megaladapis* (*Megaladapis*) are 31 and mm 35 mm respectively; the ranges are 27 to 38 mm (transverse) and 30.5 to 40.6 mm (anteroposterior). Filhol’s specimen falls well within the two ranges.

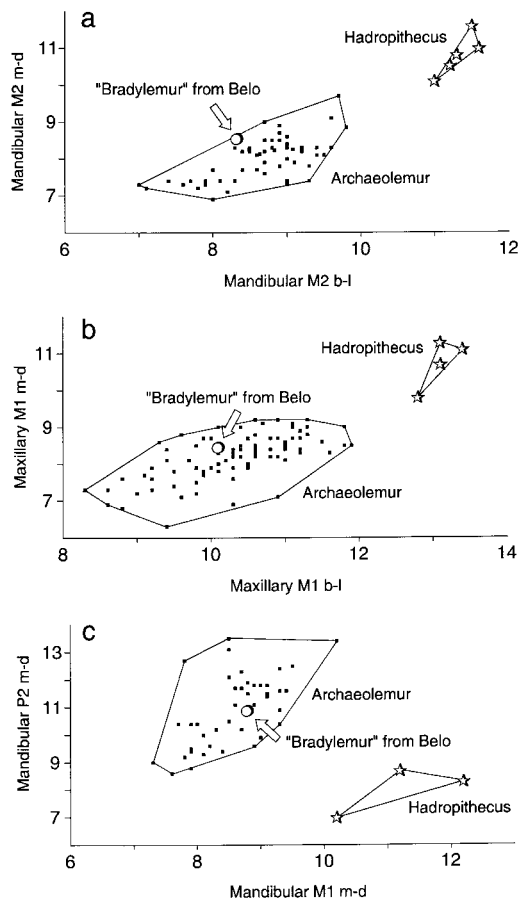


Fig. 13. Maxillary and mandibular cheek tooth dimensions of *Archaeolemur* (closed squares), *Hadropithecus* (open stars) and "*Bradylemur*" (open circles). **a:** M_2 mesiodistal diameter (Y) vs. M_2 buccolingual diameter. **b:** M_1 mesiodistal diameter vs. M_1 buccolingual diameter. **c:** P_2 mesiodistal diameter vs. M_1 mesiodistal diameter. All measurements in mm.

cubitale" (apparently, the bony bridge over the entepicondylar foramen), it seems probable that this is a specimen of *Megaladapis madagascariensis*.

Eklblom's "*Bradylemur robustus*" ulna. Eklblom (1951) described a few fragmentary archaeolemurid specimens that were found at Masinandraina,¹⁰ a site on the central highlands just east of Betafo. These specimens are in the Uppsala collection; some are figured in Eklblom's article. They include a

complete left ulna that Eklblom attributed to *Bradylemur robustus*, based on its short olecranon process, a feature that Carleton (1937) had highlighted as distinguishing the ulna of a juvenile *Bradylemur robustus*. The status of this specimen therefore depends on the status of the juvenile skeleton that Carleton attributed to *Bradylemur robustus*.

Juvenile skeleton attributed to *Bradylemur*

Carleton (1936) assigned to *Bradylemur robustus* a skeleton of an immature individual from Ampoza-Ankazoabo (west-central Madagascar) housed at the British Museum (BMNH M13924–13929). This individual, in the E.I. White collection of the British Museum, comprises two humeri (M13924) missing their proximal epiphyses but with distal epiphyses fused and capitulum present; two femora (M13925) both missing the head and distal epiphyses but with greater trochanter fused; one tibia (M13926) missing proximal and distal epiphyses; one fibula (M13927); one ulna (M13928) missing its distal epiphysis; and two ossa coxae with a sacrum (M13929). There is no associated complete skull, but skulls and mandibles from Ampoza-Ankazoabo are housed in the collections of the Paris and New York natural history museums. These skulls have been attributed to *A. majori* (Tattersall, 1973, 1982). The sample of jaws and teeth of *Archaeolemur* from Ampoza significantly overlaps that of *A. edwardsi* from central Madagascar, and indeed, the immature postcrania from Ampoza formed the basis for Walker's (1967, 1974) description of *Archaeolemur edwardsi*. Specimens from Ampoza-Ankazoabo and other sites show a wide range of variation, and this skeleton belonged to a particularly large individual. The immature specimens show none of the salient anatomical features of the specimens that we believe belong to *Hadropithecus*.

Carleton described *Bradylemur* as remarkably like *Archaeolemur* but larger in size. Her published measurements demonstrate that she did not have access to a large comparative sample. In fact, Carleton's immature "*Bradylemur*" matches the size of specimens of *Archaeolemur* from central

¹⁰He spells it Masinandraina.

Madagascar. The length of the femur (from the tip of greater trochanter to the distal margin of the diaphysis) is 179 mm; with growth to maturation and fusion of the proximal and distal epiphyses, we estimate that the femur would have been circa 190 mm in length. The humerus is 153 mm from the proximal margin of the diaphysis to the base of the capitulum; we estimate its length after fusion of the proximal epiphysis at circa 160 mm. These projected adult lengths are virtually identical to those of the "*Bradylemur*" from Belo as well as to larger individuals of *Archaeolemur edwardsi* from Ampasambazimba. The anteroposterior compression of the femoral midshaft (the ratio of femoral midshaft anteroposterior to medio-lateral diameter, expressed as a percentage) is 84.2%—again typical for *Archaeolemur* (see Table 6).

DISCUSSION

We have shown that, with the exception of one poorly described and unfigured humerus (which we believe is best attributed to *Megaladapis madagascariensis*), craniodental and forelimb materials previously attributed to *Bradylemur robustus* probably belong to *Archaeolemur* sp. (cf. *edwardsi*). However, many of the *hindlimb* specimens that have been attributed to *Bradylemur* differ in size and morphology from those of *Archaeolemur edwardsi* and probably belong to *Hadropithecus*. Accepting them as *Hadropithecus* requires rejecting Lamberton's (1938) hindlimb allocations for this species.

There are several reasons why Lamberton's allocations should, in fact, be rejected: 1) Lamberton's *Hadropithecus* hindlimb bones are virtually indistinguishable from those of *Archaeolemur* found at the same sites; 2) Lamberton's allocations give *Hadropithecus* contradictory functional signals; 3) Lamberton's hindlimb specimens appear to derive from an animal that was considerably lighter in body mass than *Hadropithecus* (judging from the skull and forelimb bones); and 4) If we accept Lamberton's hindlimb attributions for *Hadropithecus*, then we must also accept the robust hindlimb specimens described above as belonging to a new species. We are left with a new species repre-

sented by specimens of its hindlimb *only*, and curiously found at those very sites from which significant craniodental and forelimb remains of *Hadropithecus* have also been recovered (Andrahomana, Anavoha, Belo, and, probably, Ampasambazimba).

All of these problems disappear if the robust femora allocated by Vuillaume-Randriamanantena to *Bradylemur* are instead allocated to *Hadropithecus*, and the hindlimb bones that Lamberton attributed to *Hadropithecus* are recognized as belonging to *Archaeolemur majori*.

Without the hyperrobust hindlimb specimens, there is no rationale for resurrecting *Bradylemur robustus*. The type mandible and maxilla of *Bradylemur robustus*, as well as robust forelimb bones from Belo and the immature skeleton from Ampoza, are indistinguishable from *Archaeolemur edwardsi*. The existence at several western sites (Belo, Ampoza) of craniodental and forelimb specimens of *Archaeolemur* that rival the largest *A. edwardsi* from central Madagascar raises questions concerning the paleodistribution of species of *Archaeolemur*; but it does not justify the acceptance of a new genus. The taxonomic significance of this pattern of regional variation is difficult to assess without fine stratigraphic control of temporal changes in the flora and fauna across subfossil sites—a problem that is only now beginning to be addressed by field scientists (see MacPhee et al., 1985; MacPhee and Burney, 1991; Burney, 1993; Simons et al., 1995; Burney et al., in press).

The new postcranial allocations for *Hadropithecus* affect our reconstruction of this species in the following two ways. First, they allow us to correct prior apparently mistaken assessments of the postcranial proportions of *Hadropithecus* (e.g., Godfrey et al., 1995). Previous estimates of the humero-femoral length (116) and head surface area (149) indices for *Hadropithecus* are almost certainly wrong. Prior estimates of body mass based on femoral dimensions or on combined humeral and femoral dimensions (Godfrey et al., 1995) are also almost certainly wrong. Our revised estimates of body proportions place *Hadropithecus* squarely within the range of mammalian quadrupeds; they are consistent with the suite of

TABLE 8. Postcranial indices for Archaeolemuridae (new allocations) and selected anthropoids

Taxon	Humerofemoral length index	Humerofemoral head surface area index	Femoral midshaft compression index	Femoral robusticity index
<i>Archaeolemur majori</i>	85 ¹	82 ¹	84 (62)	9.7 (39)
<i>A. edwardsi</i>	82 ¹	84 ¹	83 (54)	10.2 (28)
<i>Hadropithecus stenognathus</i>	103 ²	90 ²	71 (9)	12.0 (1)
<i>Theropithecus gelada</i>	94 (9)	80 (2)	100 (2)	6.7 (2)
<i>Erythrocebus patas</i>	89 (14)	79 (6)	100 (14)	6.5 (14)
<i>Papio hamadryas/anubis</i>	88 (19)	83 (15)	99 (19)	6.5 (19)
<i>Mandrillus sphinx</i>	87 (6)	90 (3)	92 (4)	6.8 (4)
<i>Cercopithecus aethiops</i>	84 (18)	78 (6)	96 (18)	6.3 (18)
<i>Macaca fascicularis</i>	91 (29)	82 (22)	97 (26)	6.7 (26)
<i>Nasalis larvatus</i>	86 (9)	75 (9)	95 (9)	6.2 (9)
<i>Presbytis cristata</i>	78 (9)	75 (9)	99 (9)	5.9 (9)
<i>P. rubicunda</i>	68 (7)	69 (7)	95 (7)	5.5 (7)
<i>Alouatta palliata</i>	99 (7)	90 (4)	82 (7)	7.5 (7)
<i>A. seniculus</i>	95 (11)	84 (3)	85 (11)	6.5 (11)
<i>Pithecia pithecia</i>	76 (11)	77 (4)	99 (8)	5.2 (8)
<i>Pan troglodytes</i>	102 (39)	99 (4)	85 (4)	8.6 (4)
<i>Gorilla gorilla</i>	117 (27)	104 (4)	79 (4)	10.1 (4)
<i>Pongo pygmaeus</i>	130 (33)	108 (10)	77 (11)	8.9 (11)

Mean values are represented. Numbers in parentheses represent individuals in the sample.

Humerofemoral length index = (humeral length \times 100)/(femoral length).

Humerofemoral head surface area index = (humeral head surface area \times 100)/(femoral head surface area).

Femoral midshaft compression = (midshaft anteroposterior diameter \times 100)/(midshaft transverse).

Femoral robusticity index = (femoral midshaft transverse diameter \times 100)/(femoral length).

¹ Associations for giant subfossil lemur postcranial specimens collected in the early 1900s have been largely lost. Values for these indices are therefore estimated from site means (although individual associations, when known, are also used).

² These values are mixed site estimates.

morphological signals presented by individual bony elements. Unassociated materials suggest that the humerus of *Hadropithecus* was approximately equal in length to the femur, and the humerofemoral head surface area index (circa 90) was within the range of quadrupedal monkeys (80–90), and only slightly higher than that of *Archaeolemur* (circa 82–84); see Table 8. We estimate that *Hadropithecus* exceeded the body mass of both species of *Archaeolemur* and was considerably heavier than *A. majori* (Table 9). Secondly, *Hadropithecus* has been reconstructed as a semiterrestrial quadruped. The new allocations do not change this assessment. They do, however, suggest that the case for gelada- or patas-likeness for *Hadropithecus* has been overstated (cf. Jungers, 1980, Godfrey, 1988). *Hadropithecus* differed from terrestrial cercopithecids in many ways. Its relatively high humero-femoral length index and low brachial index are more reminiscent of arboreal quadrupedal ceboids (such as *Alouatta*) than terrestrial cercopithecoids (such as geladas or patas monkeys). The femoral robusticity of *Hadropithecus* is matched or exceeded within the Order Primates only by other giant extinct lemurs (some of the palaeopropithec-

ids and all of the megaladapids; see Table 10). In comparison to Old and New World monkeys with femora of comparable lengths (e.g., *Macaca nemestrina*), the femoral shafts of *Hadropithecus* are approximately twice as wide. In comparison to anthropoids with femora of comparable midshaft transverse diameter (e.g., chimpanzees), the femora of *Hadropithecus* are less than two-thirds as long. This degree of limb bone robusticity suggests a species with a stockier body build than any extant anthropoid. *Hadropithecus* has no simple anthropoid analogue.

We believe that virtually all of the giant extinct lemurs had an arboreal component to their positional repertoires. Archaeolemurids were probably the least arboreal of the lot. Nevertheless, there is ample evidence that even the archaeolemurids were adept climbers. This is revealed in both their forelimb and hindlimb anatomy (e.g., for *Hadropithecus*, the distal sites of attachment of fore and hindlimb propulsive muscles, the rectilinearity of the humeral and femoral shafts, the extraordinary robusticity and anteroposterior compression of the femoral shaft, the low brachial index, the retention of strong transverse tarsal mobility in the foot, and so on).

TABLE 9. Revised body mass estimates (in kg) for *Hadropithecus* (new allocations) compared to estimates for *Archaeolemur* and prior estimates for *Hadropithecus*

Taxon	A (Godfrey et al., 1995) ¹	B (Anderson et al., 1985)	C (Godfrey et al., 1995) ¹
<i>H. stenognathus</i>	27.1	30.1	23.3
<i>Archaeolemur majori</i>	13.9	15.6	11.6
<i>Archaeolemur edwardsi</i>	24.5	27.0	16.3
Lamberton's " <i>H. stenognathus</i> "	16.7	18.6	10.9

Estimates based on regressions derived from humeral and femoral midshaft circumferences (A and B) or femoral head diameters (C).

¹ Means of four regressions; see Godfrey et al., 1995.

A mixed locomotor repertoire can certainly be inferred for *Archaeolemur*, whose skeleton is far better known than that of *Hadropithecus*. Its numerous adaptations for ground locomotion have been described in detail and need not be repeated here (see especially Jouffroy, 1963; Walker, 1974; Jungers, 1980; Godfrey, 1988). It is also true that *Archaeolemur* was very unlike terrestrial monkeys in its overall body proportions (Godfrey, 1988); *Archaeolemur* possessed a wider trunk and shorter limbs (with more distal propulsive muscle insertions) than baboons. Its pelvis and scapula are not at all baboon-like. Its scapula is short and broad, and has a very large infrapinnous fossa.

New discoveries of the cheiridia of *Archaeolemur* highlight the extent to which *Archaeolemur* converges with baboons (Lemelin et al., in prep.). The digital proportions of the hand of *Archaeolemur* are indeed closest to those of baboons, and, as in baboons, the manual digits are short relative to the length of forelimb. The foot shares with baboons an everted set. The heads of the metapodials have dorsal steps to prevent hyperextension (suggesting that *Archaeolemur*, like *Papio*, may have been digitigrade). *Archaeolemur* also had a reduced, baboon-like hallux with somewhat limited powers of abduction. The peroneal process on the hallucal metatarsal (for the insertion of peroneus longus) is reduced, while the peroneal process at the base of the fifth metatarsal (for the insertion of peroneus brevis and abductor ossis meta-

tarsi) is large (cf. Jolly, 1972, on gelada baboons).

However, the digital proportions of the foot of *Archaeolemur* are more like those of large-bodied colobines and macaques than like baboons, with relatively longer pedal phalanges and shorter metatarsals (Lemelin et al., in prep.). Phalangeal curvature is greater in *Archaeolemur* than in baboons, further suggesting a greater arboreal component to its locomotor repertoire (Jungers et al., 1994).

Hadropithecus has been reconstructed as cursorial based on its presumed limb bone gracility (Szalay and Delson, 1979). This argument can no longer be defended. The preponderance of evidence suggests that neither *Archaeolemur* nor *Hadropithecus* was cursorial. Specializations for leaping or suspension are similarly lacking. Both *Archaeolemur* and *Hadropithecus* are best reconstructed as semiterrestrial but scansorial. They would have probably been cautious climbers; body size alone would have limited their agility in arboreal settings.

CONCLUSIONS

Lamberton's hindlimb allocations for *Hadropithecus* are highly suspect; the hindlimb specimens that Lamberton attributed to *Hadropithecus* probably belong instead to *Archaeolemur majori*. We argue that true hindlimb specimens of *Hadropithecus* exist in various museum collections and have been misidentified as "*Bradylemur robustus*" (femora) or *Megaladapis madagascariensis* (calcaneus). The rationale for resurrecting the genus *Bradylemur* (most recently defended by Vuillaume-Randriamanantena, 1982) disappears once the robust hindlimb specimens that have been attributed to *Bradylemur* are recognized as belonging to *Hadropithecus*, and the cranial and forelimb materials that have been attributed to *Bradylemur* are recognized as belonging to *Archaeolemur*. The cranial and forelimb specimens of "*Bradylemur*" from the west are indistinguishable from *A. edwardsi* from central Madagascar. New estimates for body proportions and limb bone robusticities for *Hadropithecus* demonstrate that *Hadropithecus* was considerably less baboon-like than has been suggested, and it was cer-

TABLE 10. Postcranial indices for the Palaeopropithecidae [*Mesopropithecus*, *Babakotia*, and *Palaeopropithecus*]; *Megaladapidae* [*Megaladapis* (Megaladapis), and *Megaladapis* (Peloriadapis)]; and the extant *Indridae*

Taxon	Humero-femoral index	Brachial index	Humeral robusticity index	Femoral robusticity index
<i>Mesopropithecus globiceps</i>	90 ¹	101 ¹	8.8 (7)	9.3 (8)
<i>M. pithecoides</i>	91 ¹	101 ¹	8.2 (1)	9.4 (1)
<i>M. dolichobranchion</i>	104 ¹	104 ¹	8.6 (1)	9.1 (1)
<i>Babakotia radofilai</i>	115 ¹	101 ¹	9.4 (3)	10.4 (3)
<i>Palaeopropithecus maximus</i>	152 ¹	99 ¹	7.1 (11)	12.4 (8)
<i>P. ingens</i>	153 ¹	99 ¹	7.0 (6)	12.6 (3)
<i>Megaladapis</i> (<i>Peloriadapis</i>)	109 ¹	89 ¹	9.7 (16)	14.3 (25)
<i>Megaladapis</i> (<i>Megaladapis</i>)	112 ¹	91 ¹	10.8 (9)	14.4 (11)
<i>Propithecus verreauxi</i>	53 (13)	107.7 (13)	6.7 (16)	4.8 (16)
<i>P. diadema</i>	58 (12)	110.2 (12)	7.5 (5)	5.2 (5)
<i>P. tattersalli</i>	54 (1)	108.8 (1)	7.4 (1)	4.7 (1)
<i>Indri indri</i>	54 (16)	122.9 (16)	7.1 (11)	4.8 (12)
<i>Avahi laniger</i>	49 (15)	120.6 (15)	7.8 (7)	4.6 (7)

Mean values are represented. Numbers in parentheses represent individuals in the sample.

¹ Associations for giant subfossil lemur postcranial specimens collected in the early 1900s have been largely lost. Values for these indices are therefore estimated from site means (although individual associations, when known, are also used).

tainly not similar to the patas monkey in its locomotor habits.

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NOTE ADDED IN PROOF

On a recent trip to the Université d'Antananarivo (June–July, 1997), we located in the collections of the UALPV additional hind-limb fragments that we believe belong to *Hadropithecus*. These include a distal right femur (UA8668) with a damaged medial and intact lateral condyle, as well as a proximal right tibia (UA5165) with a damaged lateral condyle and intact medial condyle. Neither specimen has site information (although each is darkly stained as is typical of specimens

from Ampasambazimba). The femoral shaft and femoral condyles are strongly anteroposteriorly compressed; the patellar groove is low and shallow. The proximal tibia is archaolemurid in morphology but linear measurements are 30-40% larger than is typical for *Archaeolemur*. New UALPV catalogue numbers have been assigned to femoral specimens A1-A8. These are: UA5155(A1), UA5156 (A2), UA5157 (A3), UA5158 (A4), UA5160 (A5), UA5159 (A6), UA5161 (A7), and AU5162 (A8).

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